
HARVARDIANA · IN · NOV · ANG
ACADEMIA
ET
VE RI
TAS
CHRISTO ECCLESIAE

Radcliffe College Monographs

No. 16

Division of Labor among Ants

BY

EDITH N. BUCKINGHAM, PH.D.

WITH A PLATE

FROM THE PROCEEDINGS OF THE AMERICAN ACADEMY OF ARTS AND SCIENCES, VOL. XLVI. NO. 18

BOSTON AND LONDON
GINN AND COMPANY, PUBLISHERS
1911

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, UNDER THE DIRECTION OF E. L. MARK. — No. 218.

DIVISION OF LABOR AMONG ANTS.[1]

By Edith N. Buckingham.

Presented by E. L. Mark, December 14, 1910. Received December 14, 1910.

Table of Contents.

[1] Published also as Radcliffe College Monographs, No. 16.

I. Introduction.

It is my purpose to state in the present paper the results of some observations and experiments on division of labor among ants, especially in relation to size and structural differences of individual workers and of classes. These studies have been carried on, with interruptions, since September, 1904, chiefly at the Museum of Comparative Zoölogy, at Cambridge, Mass., under the guidance of Dr. E. L. Mark, to whom I am deeply grateful for kind and valuable assistance, but also in part at several other places, especially in summer, viz., at the Marine Biological Laboratory, Woods Hole, Mass., at the Biological Laboratory of the Brooklyn Institute of Arts and Sciences at Cold Spring Harbor, Long Island, at Ogunquit, Maine, and at Randolph, N. H. I wish to express my obligations to Dr. W. M. Wheeler for help in identifying species and for many suggestions.

II. Historical.

Many writers have for a long time maintained that among ants there is a division of labor correlated with differences of size and structure. While some of this work has been done either by experiment or observation in the laboratory, or in the field, with this question as the main point, much of it has been more or less incidental, the student giving attention to this subject only as a side issue of other work.

There are some differences of opinion as to the functions of the

different classes. Probably this is largely due to the fact that the observations were in many cases made upon different species. There are, however, certain facts regarding the existence of classes which seem to be established by previous observations.

Different classes certainly exist in various species of ants; but the division into classes is not sharp in all species in which they are present.

Where structural differences are not well defined, there is not a sharp distinction in function: For example, classes 1 and 2 of Anomma (Savage, '**47**, p. 5); some species of Eciton (Bates, '**92**, p. 355; Belt, '**88**, p. 357); different sizes of workers other than soldiers in Holcomyrmex (Wroughton, '**92**, p. 15); some species of Camponotus (Pricer, :**08**, p. 192).

In those species where the classes are well defined, the small workers are generally admitted to be the real workers. In Anomma they engage in carrying pupae and prey (Savage, '**47**, pp. 5–11; '**50**, p. 197); in *Eciton crassicornus* and *E. vastator*, in repairing the nest, and in *E. hamata* and *E. mexicana*, in marching beside the column (Bates, '**92**, p. 362; Belt, '**88**, p. 22; Sumichrast, '**68**, pp. 43–44); in Atta, in the charge of the "razzias" (Sumichrast, '**68**, p. 44); in *A. sexdens*, in tending queen larvae and leaf-cutting (Forel, '**97**, p. 331); in *A. cephalotes*, in leaf-cutting (Forel, l. c.); in *A. structor*, in carrying in seeds (Moggridge, '**73**, p. 49); in *A. fervens*, in leaf-cutting (Wheeler, :**01**[a], p. 200); in Solenopsis, in constructing covered ways (Rothney, '**89**, p. 366); in *Pheidologeton laboriosus*, in being in the open, fighting, making covered ways (Rothney, '**89**, p. 369); in *Pheidole megacephala*, in attacking prey, carrying home prey (Heer, '**52**, p. 3); in *P. instabilis*, in foraging, excavating, caring for the brood, assisting callows to emerge (Wheeler, :**07**[b], p. 4); in Pheidole in general, in fighting, going into the field, feeding the majors (Wheeler, :**02**, p. 770); in Holcomyrmex, in harvesting grain (Wroughton, '**92**, p. 15); in *Œcophylla smaragdina*, in carrying larvae for shuttles (Doflein, :**05**, p. 502); in Camponotus, in fighting outside the nest (Forel, '**74**, p. 354); in *Camponotus ligniperdus*, *C. herculeanus*, and *C. pubescens*, in carrying larvae and pupae (Forel, l. c.); in Myrmecocystus, in fighting (Escherich, :**06**, p. 46); in *Formica sanguinea*, in all the domestic duties (White, '**95**, p. 67).

In regard to the functions of the large workers, there is evidence that they engage in a variety of occupations, but in some cases there is a great difference of opinion as to what they do. For example, in most species they appear to be for defence, since they are thus reported for Anomma (Savage, '**47**, p. 5; '**50**, p. 197); *Eciton erratica*, *E. vasta-*

tor, *E. crassicornus* (Bates, '**92**, pp. 355 and 362), *Pheidole megacephala* (Heer, '**52**, p. 3), *P. pallidula* (Forel, '**74**, p. 384), *P. instabilis* (Wheeler, :**07**[b], p. 4), Pheidole in general (Lubbock, '**77**; '**79**, p. 69; '**82**, p. 20; but Wheeler, :**02**, p. 770, says that in some species of this genus they are cowardly), Pogonomyrmex (McCook, '**79**, p. 196; Wheeler, :**05**[d], p. 384), Camponotus (Forel, '**74**, p. 354; McCook, '**76**, p. 286; Alcott, '**97**; Lüderwaldt, :**09**, p. 311), *Formica sanguinea* (White, '**95**, p. 67), Atta (Forel, '**97**, p. 331; Wheeler, :**07**[a], p. 675; Belt, '**88**, p. 83), Œcophylla (Doflein, :**05**, p. 502), and *Formicoxenus nitidulus* (Forel, '**86**, p. 132). They are said to form arches with their bodies in Anomma (Savage, '**47**, p. 5); to march beside the column in Anomma (Savage, l. c.; '**50**, p. 197), *Eciton drepanophora* (Bates, '**92**, p. 360), *E. hamata* (Belt, '**88**, p. 22), and *Atta fervens*; to perform some sort of guard duty in *Eciton mexicana* (Sumichrast, '**68**, pp. 43–44), Pheidole (Reichenbach, '**96**, p. xcv), Pogonomyrmex (McCook, '**79**, p. 196), and especially Colobopsis, the wood borers (Forel, '**96**, p. 486), in which the soldiers close the entrance of the nest with their heads and allow no strangers to enter (Escherich, :**06**, p. 46; Forel, '**86**, p. 132; :**03**, p. 83; :**05**, pp. 453–454; Wheeler, :**04**[a], p. 44; :**10**, pp. 182, 211–212; :**05**[f]; Lubbock, '**82**); to attack prey in Anomma (Savage, '**47**); to cut up prey or seeds in Pheidole (Heer, '**52**; Reichenbach, '**96**; Wheeler, :**02**, p. 770; :**10**, p. 279; :**07**[b], p. 4), Aphaenogaster and Pogonomyrmex (Forel, '**86**, p. 132); to attend to various aspects of building in *Eciton mexicana* (Sumichrast, '**68**) and Pheidologeton (Rothney, '**89**, p. 369); to care for the young in Eciton and Myrmecocystus (Escherich, :**06**, p. 46); to grind leaves in *Atta cephalotes* Forel, '**97**, p. 331); to cut grass in Pogonomyrmex (McCook, '**79**, p. 22); to carry seeds in *Atta structor* (Moggridge, '**73**, p. 49); to carry out refuse in Camponotus (Pricer, :**08**, p. 192); to pull the edges of a leaf together in mending the nest in Œcophylla (Doflein, :**05**, p. 506); to perform in general the severer duties of the colony in Formicoxenus (Forel, '**86**, p. 132) and Pogonomyrmex (McCook, '**79**, p. 22); to become repletes in Myrmecocystus (Wheeler, :**08**[b], p. 378); to lay eggs in *Aphaenogasta fulva* (Fielde, :**01**) and in Camponotus (Pricer, :**08**).

As examples of difference of opinion held by competent observers as to the function of the large workers in the same species, the following may be cited. In Atta they are thought by Bates to be passive defenders of the rest of the colony, but Wheeler contends that they are aggressive soldiers. In Pheidole generally they are thought by Lubbock to be fighters, but Wheeler states that, while in some species of this genus they are for defence, in others they are not.

In certain species there seems to be a third class, which is in size

and structure intermediate between these two, while in function it sometimes resembles the large and sometimes the small.

Often the same occupation is seen to belong to one class in one species and to another in another species.

That in general the greater amount of work is done by a few workers is the contention of Miss Fielde (:03[d], p. 621) and of Forel ('74, p. 151). Lubbock ('82), working on foraging in *Formica fusca*, came to the same conclusion, but made no study of the relation of activities to size. Pricer thinks that in Camponotus it is the medium-sized ants which accomplish most, whereas Forel believes that the small ones do the most work. But I know of no case where in a given species a large number of functions have been studied in relation to class distinctions.

Therefore without further evidence we are not in a position to state definitely the relation of size and form to division of labor.

III. Polymorphism of Ants.

A. Polymorphism in General.

In order to study satisfactorily the correlation between polymorphism and division of labor, it is necessary to define what is meant by polymorphism. Wheeler (:10, p. 86) says that only those animals properly represent the phenomena of polymorphism "in which characteristic intraspecific and intrasexual groups of individuals may be recognized, or, in simpler language, those species in which one or both of the sexes appear under two or more distinct forms."

According to Wheeler (see also Wheeler, :07[b], p. 85) and to Escherich (:06, p. 45) polymorphism is commonly supposed to be due to a physiological division of labor.

Though both sexes of ants show some tendency to polymorphism, such as is described for males by Wheeler (:04[d]), by Forel (:04[a]; :04[b]), and by Emery ('86; :06), polymorphism is not common in the male sex, and we are not here concerned with that manifestation of it. If, however, we confine our attention to the females of a colony of ants, it will be found that they are, as a rule, markedly polymorphic, consisting of two chief divisions, queens and workers; although in some cases (certain Ponerinae) there are no apparent distinctions between the queen and the worker classes, the two forms being connected by individuals of an intermediate character (Wheeler, :00[a], p. 1; :10, pp. 242–243). Wheeler (:00[a]) feels certain "that forms externally indistinguishable from the workers commonly function as females." Again, he (:03[c], p. 6) says of *Leptothorax emersoni* that many workers approach the queens in size, possess ocelli, and probably function as

queens. In *Leptothorax tuberum*, Fletcher ('89) found that workers lay eggs. Workers, though very rarely, may even bear vestiges of wings (Wheeler, :05ᵉ). Emery ('94, p. 54), too, states that in most Ponerinae the workers are only slightly differentiated from the queens, and that in several species there are intermediate forms between workers and queens. Furthermore, that some species have a wingless queen which is transitional between the queen and workers. Such a queen is also mentioned by Wheeler (:04ᵉ, p. 251). Moreover, the head of the normal, winged queens of such ants as have two different sorts of workers is almost always less developed than that of the largest worker (Camponotus, Pheidologeton, Pheidole, etc.); only seldom (certain Colobopsis and Cryptocerus) does the head of the queen resemble that of the largest worker in size and form. It furthermore appears (Emery, '94, p. 55) that the degree of development of the sexual glands is correlated with the development of the head.

As a rule, however, egg-laying belongs to the queen, while the workers attend to the general needs of the nest, though some workers do occasionally lay eggs. In a good many species they seem, according to Miss Holliday (:03), to be anatomically if not physiologically adapted for this. Indeed, Wheeler (:06ᵃ, p. 298) says that when workers are well fed, they readily become fertile, and that they can, and often do, produce normal young from unfecundated eggs. But if the workers may lay eggs, so, on the other hand, according to Wheeler (:03ᵃ), "the females [Leptothorax Mayr] live almost like the workers, being merely somewhat less inclined to work." But in some cases (e. g. in *Formica consocians*, *difficilis*, *sanguinea*, etc.) the queen has so far lost her powers of performing the general work of the nest that she is dependent on the workers of another species to bring up her first brood (Wheeler, :04ᵇ, p. 359; :04ᶜ; :05ᵃ; :05ᵇ; :05ᵈ, p. 399), and it is doubtful whether in some species she alone could found a colony (Wheeler, :05ᵃ). Again, through becoming parasites, the workers of some species in several genera (Anergates, Epoecus, Tomognathus, Sympheidole, Epipheidole) have secondarily disappeared (Forel, '95, p. 145; Wheeler, :04ᵈ).

Nor are the workers of a given species themselves always alike. Emery ('94), Wheeler (:07ᵇ, pp. 53–57; :08ᵃ, pp. 44–47; :10, pp. 92–99), and Forel ('95, pp. 142 et seq., and :04ᵃ) describe several castes of females in many species, and these authors would account for the great gap between the extreme types of workers in a species by the disappearance of intermediate forms (Emery, '94; Wheeler, :08ᵃ, pp. 58–59; :10, p. 112; Forel, '86, p. 132; '95; :04ᵃ, p. 574). On the other hand, there are species in which there is still a completely graded

series from the smallest to the largest workers (see also Emery, '96, p. 397).

Occasionally the fertile winged queens (Emery, '96, p. 399) are of different sizes, as, for example, in *Camponotus abdominalis* F. and *C. dorylus* subsp. *confuscus* Emery; and the differences here are parallel to those of the workers. Again (Wheeler and McClendon, :03; Wheeler, :03[b]), some species may have two distinct forms of queen without intermediates, and Wheeler (:03[b], p. 650) is inclined to believe this due to mutation. Moreover, intermediates, though usually abnormal, are found between the queen and the largest workers (see also Forel, :04[a], p. 574; Wasmann, '90, pp. 301 et seq.; '95; :02; :09[a], pp. 46, 52, 60, et seq.; Viehmeyer, :04; Muckermann, :04; and Wheeler, :01[b]; :10, pp. 406–408). Hence, taking ants as a whole, there is evidence of a long series of gradations from the smallest workers to the largest queens.

When there are modifications of workers of the same species, they are (Emery, '96, p. 398), first, modifications of size with but slight differences of form of body and mandibles; but on approaching the maximum size the form of the mandibles changes rapidly, though by a series of gradations. Individuals showing such gradations are difficult to get together because of the scarcity of soldiers, and especially of forms intermediate between them and the worker-major. There are also differences of form and sculpture of the head and other parts of the body. According to Forel ('95, p. 143), the large worker may be distinguished by its enormous increase in size or by the peculiar form of its head or its mandibles, which are suited to breaking seeds, obstructing the nest opening, or fighting, etc. If the head has no such adaptation, the ant shows no peculiarities.

Wasmann ('90, p. 300) says that with differences of size are correlated differences of sculpture of separate parts of the body, but especially of the back and the head. Emery (:01[a]; :01[b], p. 54, foot-note, and :04, pp. 588–589) states that the smallest forms of driver ants, as well as of other species of Dorylus, differ in the structure of the head and its appendages, even in the number of antennal joints, from the medium-sized and small ants, and that these differ from the largest specimens in having smaller heads and toothed mandibles.

It is an interesting fact, as Emery ('94, p. 55) points out, that in the Ponerinae, which are considered morphologically as the stem form of ants, there is no striking polymorphism of the worker classes (Emery knows it only in the case of Melissotarsus). But polymorphism of the worker does appear in many genera of all the other groups, and it therefore seems that polymorphism among ants has originated polyphy-

letically. It is furthermore probable that, since the large workers more closely resemble the queen, they are more primitive than the small ones. Emery, then, classifies ants according to the condition of the workers as follows :

I. Ants with only large workers.

II. Ants with large and small workers.

a. The extremes connected by intermediate forms.

b. The large and small workers without intermediate forms.

III. Ants with only small workers, which are very different from the queen ; due to dropping out of large workers.

IV. Ants with one kind of workers, which are smaller than the queen through increase of size of queen.

V. Ants from which have disappeared the worker class because of parasitism.

According to this classification, only the species which fall within the second group offer more than one form of workers in the same species. Hence, I have chosen as examples of workers with extremes connected by intermediate forms, two species of Camponotus (*C. americanus* and *C. herculeanus pictus*). As the only available species in this region of the country which falls under the division "large and small workers without intermediate forms" is *Pheidole pilifera*, I have also selected that species. In addition, I succeeded in collecting *P. vinelandica* from New Jersey, and in obtaining *P. dentata* through the kindness of Mr. Carl Hartman of Austin, Texas.

B. Polymorphism of the Species Studied for Division of Labor.

1. *Camponotus.* — In Camponotus the workers form a continuous series from the smallest, which have heads much longer than broad, to the largest, whose heads are nearly as broad as long. This was established for *Camponotus americanus* by measuring nearly 500 individuals, most of which were alive. To secure significant and reliable results requires the selection of suitable and easily identified points on the head and careful attention to the *position* of the parts during measurements. In using the microscope to view the head and to get the distance between points in its outline it is especially necessary to have the heads of the individuals which are to be compared with one another held in the same relative position. It was found practicable to do this by pressing the head firmly into a small mass of rather soft bees' wax mounted on a glass slide. Usually the wax thus employed held the head in the desired position, but sometimes it was found necessary to push the fore feet of the animal also into the wax to prevent the ant from pulling its head away. The aim in orienting the

head was to place it as nearly as possible in a horizontal position for the purpose of viewing its dorsal aspect. This was done in the case of the transverse axis by placing the head so that the outer margin of the two eyes was equally distant from the outline of the adjacent side of the head; in the case of the anterio-posterior axis, by bringing the anterior margin of the clypeus and the posterior margin of the head to lie at the same focus. These two points can both be seen distinctly

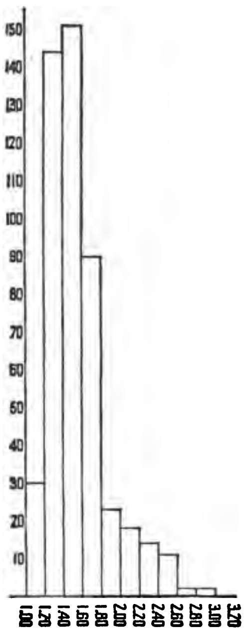


FIGURE 1.

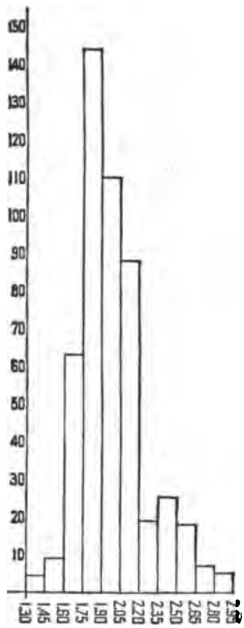


FIGURE 2.

only when the head is in one position. In making the measurements I used a Zeiss A* objective so set as to give a magnification of about 45 diameters at a projection distance of 430 mm. With this arrangement the whole length of the head of the largest individual could be covered by the ocular micrometer, by means of which the measurements were made. To avoid accidental errors measurements were taken more than once, and recorded in terms of divisions of ocular micrometer. In all cases they were ultimately calculated in millimeters. By "length" is meant the distance measured in a straight line in the median plane between the posterior margin of the head and the

anterior margin of the clypeus; by "breadth" or "width" is meant the distance between the lateral outlines of the head measured along a line tangent to the posterior margin of the eyes.

The first diagram (Figure 1) is a frequency polygon, giving the results

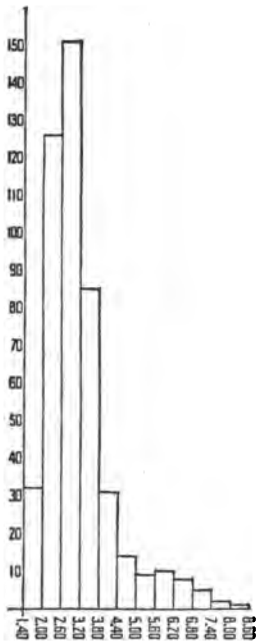


FIGURE 3.

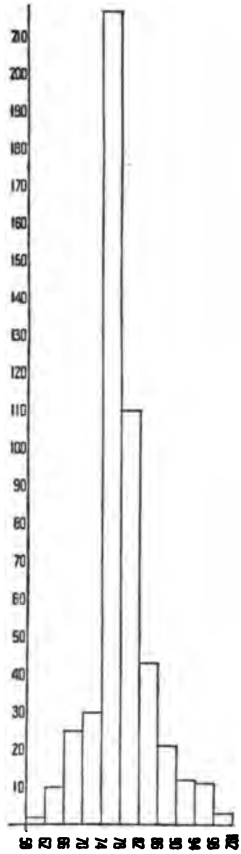


FIGURE 4.

of the measurements of width, Figure 2 that of length, Figure 3 that of length multiplied by width, and Figure 4 the ratios found by dividing width by length. In constructing the polygons the ants were divided into classes. For the length a difference of 0.2 mm. was chosen as the basis, the first class containing all individuals in which the length of

the head fell between 1.00 mm. and 1.20 mm.; the second class between 1.20 and 1.40 mm., and so on. The interval adopted for width (Figure 2) was 0.15 mm.; that for area 0.6 sq. mm.; and for ratios 4 per cent of length. The ordinates show the number of individuals falling within each class. None of the resulting "curves" shows any signs of two or more maxima, except that of Figure 2, where the indication is too slight to be of significance, so that there is no evidence from these measurements that there are well marked classes. When a given colony was plotted by itself, the results were substantially like those here recorded for the combination of several colonies, and each curve was therefore similar. Consequently it seems to me that no objection can be raised to combining the results of several colonies, as I have here done.

I have also tried to find evidence of distinct types or classes based on other grounds, such as the number of teeth on the mandibles and the ratio of the width between the eyes to the width between the insertions of the antennae, but with equally small success.

I next turned my attention to *Camponotus herculeanus pictus*. Here, too, although I did not make such measurements as are described above for *C. americanus*, there seems to be a complete, graded series. This fact is easily seen from the Plate, which was made from a series of photographs taken with the aid of a microscope. All exhibit the animal in the same position and under the same magnification, — about 9 diameters, — so that they represent accurately variations of size and shape. But not relying on this single view of the head, since all the parts were not visible in that position, studies were made with the microscope from different sides. When necessary in comparing the size of the various organs measurements were made by means of the ocular micrometer.

1. The most striking difference (Plate, Figures 2–20) between the large and the small worker is that of size, the heads of the large workers being not only actually but also relatively larger than those of the smaller ones.

2. Not only is the head of the larger workers larger, but it is also of a somewhat different shape. Thus, while the head of the small worker is somewhat longer than broad, the head of the large worker is more nearly equal in the two dimensions, or even a little broader than long in the largest specimens, thus resembling *Camponotus americanus*. Moreover, the posterior margin of the small heads is convex backward, whereas that of the large workers is more nearly straight, or even slightly concave backward. It might be more nearly correct to say of the latter that it presents a backward convexity of the two ends of the pos-

terior margin, probably due to the greater development of the great jaw muscles, as in this respect the large worker seems to resemble the condition of the soldier in those species where there is a real soldier. Moreover, there is another difference in the general shape of the head, in that its greatest diameter dorso-ventrally is less in proportion to the length of the head in the larger workers; in other words, the heads of the larger workers are somewhat shallower.

3. In regard to the differences of some of the organs of the head, it may be seen at a glance that the length of the antennae relative to the size of the head is much less in the larger ants, they being hardly any longer by actual measurement than in the smaller ants. The number of joints in the antennae seems to be here, as in *Camponotus americanus*, always the same, unlike Dorylus (Emery, :01[a]). There are, however, some differences in the antennal parts. For example, in the smaller ants the scape is slightly longer than the width of the head, while in the larger individuals it is somewhat shorter. In heads of intermediate size the condition is variable; sometimes the head is wider than the length of the scape, sometimes the reverse is true, regardless of the size of the head. In the larger ants the funiculus is only slightly longer than in the smaller ones, and in proportion to the size of the head it is much shorter. In proportion to the length of the scape it is shorter in the larger ants. The scape itself is also of a different shape in the two extremes; in the large ants it is larger at the distal end than at the proximal end, whereas in the small workers it is nearly uniform in thickness throughout its length.

4. Again, it was found that in the larger ants the compound eyes are set slightly further back, as may be seen especially in side view, and that they are also somewhat further from the margin of the head.

5. The clypeus presents a good deal of difference in the two extremes; in the larger ants it is much thinner dorso-ventrally and only slightly arched on the dorsal surface, while in the smaller ants the arch becomes higher and more angular. Moreover, there is a considerable difference, as seen from the dorsal side, in the shape of its outline, which is nearly rectangular in the large individuals, and somewhat hexagonal in the small.

6. In the larger workers the frontal carinae (Wheeler, :10, p. 18) are slightly farther apart in proportion to the total length of the head.

7. The mandibles are not very unlike in the two extreme sizes, but are, on the whole, more strongly built in the large workers. All the teeth are fairly large in the large workers, but in the small workers the outside ones are the stronger, though the difference in strength is not great.

8. But in each of these characteristics there is a graded series, so that a distinction into classes cannot be made; indeed, it sometimes happens that in a single individual of the middle size some characters more clearly resemble those of the large workers, while others are more like those of the small. These observations tend strongly to confirm those made by measurements on *Camponotus americanus.* They are, so far as I am aware, the only observations of the sort made on this genus.

In order to see how much the *queens* (Plate, Figure 1) of *Camponotus pictus* differed from the *workers* in regard to these same structures, I made similar observations on them, comparing them with the largest workers, which it is evident they more closely resemble than they do the small ones. The results follow:

1. The head of the queen is here somewhat, though not much, larger than it is in the largest worker. In regard to its shape, as compared with that of the worker, it is only slightly broader in proportion to its length, about as much as we should expect from its increased size. The posterior margin of the head of the queen resembles very closely that of the largest worker. The dorso-ventral axis of the head is slightly shorter than in that of the worker.

2. The length of the antennae, in proportion to the size of the head, is less in the queen. The antennal joints are of the same number in worker and queen. If the length of the scape is compared to the width of the head, it is found that in the queen it is hardly, if any, shorter than in the large worker. The funiculus of the queen is slightly shorter in proportion to the length of the scape. In proportion to the size of the head it is also somewhat shorter, being actually of about the same length in both forms. The scape in the queen is still thicker at the distal end than in the large workers.

3. The compound eyes are slightly further back than in the large worker, and resemble the condition in the small worker more closely in being a little nearer the margin than in the large worker.

4. The clypeus is even flatter in the queen than in the large worker and slightly more indented by the cheeks; the arch is curved in both.

5. The frontal carinae are slightly further apart in the queen than in the large worker.

6. The mandibles of the queen very closely resemble those of the large worker.

So far, these characters make it appear as though the queen were merely at one end of a long series of females. But in this species other characters, such as the more developed ovaries, the presence of wings, etc., show that there is a noticeable break between the queen and the largest worker.

However, in nearly all the differences among the workers of this species, it is necessary to observe that there is no break in the series, no tendency to form separate classes. There is, rather, a continuous variation from one size to the next, forming, as Wheeler (:07[b], p. 77) says, a series of intermediates between the very large and the very small.

Although one would not expect the duties of classes in this species to be as distinct from one another as they are in those polymorphic species where there are sharp morphological differences, still it seemed possible that polymorphism might be associated with some recognizable division of labor. Furthermore, as already stated, it was thought well to compare the activities of two forms, in one of which (as in *Camponotus americanus* and *C. pictus*) there is a graded series; and in the other (as in certain species of Pheidole) there are dimorphic classes without intermediate forms between the large-headed soldiers and the workers (Emery, :02, p. 719; Wheeler, :10, p. 559).

2. *Pheidole.* — In Pheidole there is, as a rule, no intermediate form between the small workers of ordinary proportions and the soldiers (Emery, :02, p. 719; Wheeler, :10, p. 559), though such intermediate individuals are occasionally found. By "soldier" is meant, according to Forel ('95, p. 143), merely a large worker which, through complete dropping out of the intermediate forms and through adaptation to precise functions, has become differentiated from the small worker. It is often so different from the worker proper as to be taken for another species. In some species, as *Ponera edouardi*, there are, indeed, two forms of soldier (Forel, '95, p. 145). In Pheidole, however, there is only one. The differences between the heads of the soldier (Plate, Figure 22) and the worker (Figure 23) of *Pheidole pilifera* may be described as follows:

1. A great difference in the size of the head, that of the soldier being much larger, not only actually, in correspondence with its larger body, but even relatively; it is so heavy and clumsy, that it is held bent downward at a much greater angle than that of the small worker.

The thickness of the heads measured dorso-ventrally does not differ materially. When the dorsal surface of the head is examined, however, it is found that the proportions of its outline are quite different; it is nearly square in the small workers, and quite oblong in the soldiers. The posterior margin is only slightly cordate in the small ants; but in the soldiers it is deeply indented in the centre, where ends a median dorsal groove, which begins about the middle of the head. This groove lies between the muscles of the mandibles, which cause a pair of longi-

tudinal mounds; these are wanting in the small workers. The head of the soldier is much redder, except for the black eyes and the dark regions around the mouth. It is also covered with stronger ridges of chitin and is more pubescent.

2. The antennae are, relatively to the whole head, much longer in the small ants. The number of joints is the same for both classes, but in the small ants the three distal joints are larger than in the soldiers. The scapes are in form very similar in the two castes, but are relatively shorter in the soldier. The funiculus, although actually slightly shorter, is, in proportion to the size of the head, much longer in the small workers.

3. The frontal carinae differ slightly in the two forms, being nearly parallel in the small workers, but diverging posteriorly somewhat in the soldiers.

4. The clypeus in the small ants resembles a triangle, somewhat curved outward in front, but in the soldier it has four sides, of which the two lateral diverge anteriorly, and its anterior margin is slightly notched in the middle.

5. The compound eyes are further forward in the soldier than in the worker.

6. The mandibles in the small ants are slender, and bear teeth, of which the outside one is especially large, but in the soldier they are very strongly built, blunt, straight-edged, without teeth, and somewhat sharp on the edges which come in contact with each other, very much resembling hatchets.

When the queen (Plate, Figure 21) of this species was examined, it was found that, while she resembles the worker more closely in certain characteristics, she is, on the whole, more like the soldier.

1. Her whole body is larger than that of the soldier, suggesting that, as in *Camponotus americanus* and *C. pictus*, she represents one end of a series from which some members have, probably, dropped out. But there is more difference between majors and queens in this species than in Camponotus, and even within each of the two classes, soldiers and minors, — supposedly connected by missing forms, — the gradation is not as uniform as it is throughout the Camponotus series.

2. Her head is both relatively and actually smaller than that of the soldier. On the other hand, the shape, both in regard to its general proportions and to the posterior margin, more nearly resembles that of the worker; but the chitinous ridges and the general color closely resemble those of the soldier, though they are less marked.

3. Certain organs of the head also resemble those of the soldier more closely, viz., the antennae and their parts, the angle which the

frontal carinae make with each other, the shape of the clypeus, and the pubescence, this being even more marked than in the soldiers.

4. On the other hand, the mandibles are toothed and in shape are much like those of the small workers, and the mandibular muscles do not cause mounds on the dorsal surface of the head.

5. There are three well marked ocelli, and the compound eyes are much larger than those of either soldiers or workers.

6. From these facts it seems probable that the large workers originally resembled the queen more than did the small workers, and later developed to an exaggerated extent certain of her characteristics, which the small worker, on the other hand, lost.

IV. Methods in General.

In order that I might not be biased when considering the subject of division of labor among ants as a whole by conclusions deduced from a single method of work, it was thought well to make observations under several different conditions, partly by placing the ants in more, partly in less natural surroundings. My observations may thus be arranged in three groups as follows: A. work with Fielde (:00; :04[a]) nests, with aluminum nests (Buckingham, :09) and other apparatus; B. Work with Barth (:09) nests; C. Out-door work.

A. *Work with Fielde Nests, Aluminum Nests and Other Apparatus.*

The Fielde and aluminum nests used are shown in plan in Figure 6 (p. 447); they were ten inches long and six inches wide.

1. *Marking.* — In order to study the activities of each member of a colony, when experimenting with ants in the Fielde nests and in my own, the following method was employed: Each individual was marked and its head measurements were recorded together with the data of the various experiments, so that it might be possible to tell which sizes were concerned in the different activities and to keep account of the special activities of each individual. Length of head multiplied by width of head was used as a criterion of size. The classes of the species of Pheidole which I used are so distinct that I have thought no marking necessary, and have simply recorded the numbers of ants of each class taking part in each activity. With Camponotus, however, the case was quite different, since it was impossible to establish natural groups or classes, owing to the continuous gradation of the forms into one another.

A common way of marking ants, described by Miss Fielde (:03[a], p. 610, foot-note), is to affix to them colored paint by means of var-

nish. I have never succeeded in making this method work well, since the paint often falls off or is removed by the ant or its companions. Especially is this likely to happen in the course of experiments extending over considerable time, as mine have done. I have had no better success with trying to affix other substances to the ants. The following

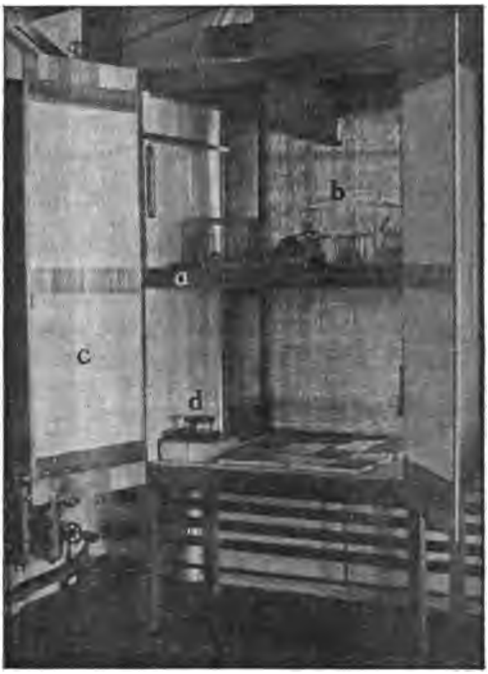


FIGURE 5.

method, however, works well with species of large ants: Pieces of colored sewing-silk were split into their component strands. One or, if different colors were to be combined, two or more of these were tied with a single knot into a loop. The legs of the insect were then grasped by the thumb and forefinger of the left hand, while with the right hand the loop was slipped over the abdomen, adjusted immediately back of the last pair of legs, and fastened by completing a square knot, care being taken not to make the loop around the ant too tight. A small pair of forceps is indispensable in adjusting and tying the loop. Provided that the thread is sufficiently slender, I cannot

see that its presence makes any difference in the behavior of the ant after the first few minutes, and the number of individuals which can be thus marked is practically unlimited, for by varying the single or combined colors, many different combinations can be secured.

2. *Heating.* — In carrying out this set of observations the ants were kept during the summer at ordinary room temperature. In winter, however, in order to maintain a state of greater activity than they would have had at room temperature, especially at night, it was deemed expedient to keep them at temperatures which approximated those of summer, the extremes being about 60° and 90° Farenheit. They were therefore placed, when not under observation, in an artificially heated chamber (Figure 5). This chamber, made of matched boards ⅞ in. thick, was about five feet high, three and a half feet wide, and two and a half feet from front to back, and raised on wooden legs about two feet above the floor. The front of the chamber was composed of two doors (*c*), and the back was open, but was placed against the wall of the room in such a way as to surround a west window that was provided with two sashes enclosing an air space between them. The floor, the roof, the two ends and the two doors were lined with sheets of asbestos. To give more surface on which to place the nests and to allow at the same time free circulation of the heated air, a shelf (*a*) made of slats was placed midway between the floor and roof. Since the afternoon sun sometimes made the temperature in the chamber dangerously high, and since daylight excites ants, the window was supplied with a red curtain (*b*), so arranged that it could be easily raised or lowered. The curtain was used continuously except occasionally for a few moments when a little extra light was needed while caring for the ants. Although the doors could be tightly closed, they were usually left slightly ajar, thus affording better ventilation and avoiding danger of too great a rise of temperature. Heat was supplied by an electric stove (*d*), the current being taken from the lighting circuit. The ants which I was studying were kept on the floor of the chamber, where the temperature was somewhat lower than on the shelf. The latter was used by Mr. I. A. Field for the ants he was rearing in connection with his studies on spermatogenesis. The chamber was built for receiving ants and in accordance with plans worked out by Mr. Field and the director of the laboratory. While the ants were kept in this chamber at such times as they were not under immediate inspection, all observations were made at ordinary room temperatures, under the influence of daylight.

B. *Work with Barth Nests.*

1. *Environment in General.* — It appeared that there are some activities of ants which cannot be satisfactorily studied in natural nests, and in order to watch the insects under more natural conditions than were used for observations under division *A* (pp. 440–442), and to subject them, though in the laboratory, to an environment as nearly as possible resembling that of their wild homes, Barth (:09) nests were selected. Here the ants soon burrowed their chambers and galleries in earth between two glass jars, a smaller set within a larger, the outside of which was always covered with thick black paper, except at such times as the nests were examined. To prevent the escape of the ants, screens of wire gauze were placed over the tops of the jars, which were otherwise open, allowing free access of air. During the period that these observations were made the nests were kept continuously in a photographic dark room, with black walls, and a small window through which daylight entered for some hours each day. In order to produce the darkness normal to ants underground, this daylight was closed out when the black paper was removed from the nests during observation. The light needed in studying the movements of the ants was secured by a 16-C. P. incandescent filament enclosed in a bulb of ruby glass. This lamp served also another purpose, viz. to stimulate the ants slightly, and thus make them more lively.

2. *Influences of Heat and Light.* — That this stimulus was due to heat and not to light was proved by the following experiment, tried on two different colonies of *Camponotus herculeanus pictus.* The results of both were so nearly alike that I give only those of one. When the temperature of the earth in the nest was 20° C., by a thermometer previously placed there, and the ants were quiet, a water screen 2½ inches thick was placed between the nest and the ruby bulb, which was about four inches distant from the nest. After five minutes the ants were still perfectly quiet. The screen was then removed. Immediately the ants began to move vigorously, and at the end of five minutes more the glass felt warmer to my hand where the light shone on it than in other places. The temperature in the earth near the ants had now gone up to 22° C., and the ants were carrying the larvae toward the outer glass of the nest. The water screen was now replaced, and the ants examined again at the end of another five minutes, when, though the thermometer still registered 22° C., the ants were perfectly quiet. After five minutes more with the screen still in place, the room having become in general warmer, the thermometer in the earth registered 22+° C., and the ants were perfectly quiet. Black paper

was now placed around the nest to keep out the light, the lamp being left in the same position, but the screen having been removed. After five minutes the thermometer reading was 25° C., and the ants were in commotion. I then poured cold water over the outside of the nest till the ants became fairly quiet, the thermomoter standing at 22.5° C. When the thermometer had reached 20° C., the lamp was again placed near the nest, and at the first intimation of motion among the ants a reading of the thermometer was taken; it showed 21° C. But previously, when there was light and no *rise* of temperature the ants were quiet at 22+° C. The nest was now cooled to 19° C. and the ants began to move at 20° C. It therefore seems fair to assume that the stimulus is not simply heat, but a *rise* of temperature. To see the effect of light other than red, at the same power, a 16–C. P. incandescent lamp with an ordinary glass bulb was now used, at the same distance that the ruby light had previously been, with the water screen in place. At the end of two minutes the ants were disturbed, but they seemed to be less disturbed by the light of a 16–C. P. incandescent lamp than by its heat. From these two experiments it seems clear that we are dealing here with the stimulus of heat from the ruby bulb rather than of light. Heat is really a natural stimulus to ants, as they are in the habit of coming up under stones or to other warm parts of the nest, and of taking there the eggs, larvae and pupae to warm them. Moreover, in the Barth nest I found that so long as the heat was not too intense, the ants took their young toward it; if, however, it became very intense, from placing the lamp nearer the nest, they carried them away. So long as the behavior of the ants indicated that the warmth was favorable to them, so long, I think, we may safely say that it was a natural stimulus.

C. Out-door Work.

That I might study ants under entirely normal conditions, I worked during the spring, summer, and autumn of 1909 on out-door colonies of *Camponotus herculeanus pictus* at Randolph, N. H., and of *Pheidole pilifera* at Cambridge, Mass. In order to obtain as natural results as possible, the observations were made in many cases without touching the nest at all, and in no case was there any disturbance of the ant when it could be avoided. To this end, before making observations, I often waited for a time after seating myself on the ground so that the ants might recover from any stimulus to activity caused by my approach. In making notes or in preserving ants, all individuals sharing in any activity under the influence of any excitement, other than that which

might naturally be expected in such an activity, were so recorded. To gain as much evidence as possible from the observations, two methods of study were used, viz. (1) field notes, and (2) captured ants.

1. *Field Notes.* — First, at the time the observations were made notes were taken, giving general impressions of the sorts of individuals engaged in various pursuits, and these notes were later carefully summed up and compared for the different colonies. Although such notes are necessarily in many respects less accurate for Camponotus, because of the nature of polymorphism in the species here used, than is the evidence derived from the second method, to be described below, yet they reveal more precisely the numbers of ants engaged in the various activities, and are, I think, in the main fairly correct.

2. *Captured Ants.* — The second method employed in the field work, used particularly in connection with *Camponotus herculeanus pictus*, was as follows: Because the workers of this species form a graded series (p. 438), it was in many cases impossible to judge with accuracy as to the size of ants engaged in particular activities, and it was, therefore, thought well to distinguish, for the purpose of later study, those ants which shared in any given activity. Accordingly, small vials of commercial alcohol were used, into each of which were dropped all ants of a particular colony engaged in a given activity on any day, and each bottle was provided with a label giving the colony, the activity, and the date of capture of all ants contained therein. For convenience each ant was later mounted on a separate pin with a label containing the above data.

D. Activities Tested.

Although the activities of the ants studied have not all been tested with each method of observation, some of them have. I give here the whole category of activities which were examined by any method: 1. foraging, either (*a*) presence in the field, or (*b*) actually carrying food; 2. partaking of different foods; 3. feeding themselves; 4. regurgitating food to others, likewise receiving regurgitated food; 5. licking others, likewise being licked; 6. tending the young (eggs, larvae, or pupae); 7. building, (*a*) digging, (*b*) carrying earth; 8. carrying other ants, likewise being carried by other ants; 9. surrounding the queen; 10. fighting; 11. responding to disturbances of the nest; 12. guarding; 13. scavangering.

Though the nature of most of these activities seems clear from the names given them, a few, perhaps, need explanation. For example, "preparing food" means tearing it into smaller pieces or crushing it

so that it can be carried into the nest, or so that it is suitable for eating. "Regurgitating food" is a fairly common habit among ants; when they have been feeding, they sometimes disgorge some of the food to their companions. The process of "licking" is minutely described by McCook ('79, p. 125) for *Pogonomyrmex barbatus* as cleaning each other. The ant which is doing the licking or cleaning passes all over the body of the other ant with her mouth parts, which are constantly in active motion. The ant which is being licked stands still, apparently content to have the process carried on. Wheeler (: 03[c], pp. 43–44) says in regard to licking in Leptothorax that there can be little doubt that the ants obtain some substance from the body of the Myrmicas, but it is difficult to ascertain its nature. He thinks it may be a secretion of the cutaneous glands, or merely the salivary secretion that has been spread over the Myrmicas by the mutual licking in which they indulge. Later he (Wheeler : 07[c], p. 70) speaks of it as an "oleaginous secretion." By "responding to disturbances of the nest" I mean such disturbances, for example, as knocking on logs in which *Camponotus pictus* for the most part lives, jarring the artificial nests, or tearing open log nests or earth nests. "Guarding" signifies such habits for the protection of the nest as are found in Colobopsis (see p. 428). Although these guards allow all the inhabitants of the nest free passage, they nevertheless keep out all intruders.

V. Studies of Camponotus.

A. Camponotus americanus.

In the observations on the various activities of *Camponotus americanus* I have tried to discover (1) the proportion of the whole number of worker ants which engaged in a given activity, (2) the extent to which each individual was engaged in that activity, and (3) the relation, if any, between the size of the individuals and the nature of their activities.

1. *Foraging.*

1. *Methods.* — In order to determine to what extent this species is attracted by food near at hand, and which individuals respond to this stimulus, any arrangement which would allow one to know definitely which individuals, if any, had had recourse to the food (or at least to the chamber containing it) during a fixed interval of time would afford a basis for judging of the general effect of food as a stimulus and for determining the particular ants or classes of ants stimulated by it. The method adopted to attain these ends was as follows: The ants

were confined in the Fielde nests already mentioned (Figure 6). In all cases the chambers were connected with each other by two passages, one at each end of the partition. In each of the chambers was a moist sponge, and both chambers were kept moderately dark by pasteboard covers laid over the glass. The ants were placed in chamber *A*, the food in chamber *B*. One of the passages between *A* and *B* was blocked by a plug of cotton, while in the other was placed a trap-door which allowed the ants to pass from *A* to *B*, but not in the reverse direction. The trap-door (Figures 7–11) was made as follows: A piece of mica, *a*, slightly narrower than the passage, rested on a fulcrum, *b*, in such a way that one end touched the floor of the nest in chamber *A*, while the other came against the roof (*c*) of the passage in chamber *B*. The roof, *c*, covered the whole passage between *A* and *B*. In Figure 8, a front

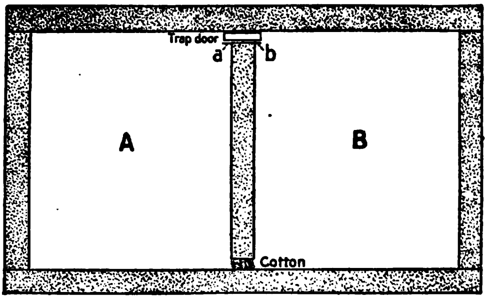


FIGURE 6.

elevation, are shown, besides the parts already mentioned, *d*, the outside wall of the nest in cross section, and *e*, the cross partition between *A* and *B*, also in section. The fulcrum (*b*) consisted of a short piece of straightened watch spring just long enough to fit easily across the passage, and supported, edge up, between two strips of thin card-board, cut as shown in Figure 9, where *b* is the steel watch spring, and *h* one of the supporting cards. The dotted lines (*g*) show where the card was bent at right angles to form the parallel wings, *f*, which were glued to the glass wall of the passage (Figure 8, *d* and *e*). The portions *i* of the card-board remained in a plane parallel to *b* and hence perpendicular to *f*. Both edges of the mica plate (*a*) were notched at the middle (Figure 11) to receive the projecting edges, *i*, of the vertical card-board. This arrangement prevented the slipping of the mica plate on the fulcrum, while allowing freedom of motion in a vertical direction. The two arms of the mica plate were of unequal length, the longer and

heavier arm projecting into chamber *A*. Consequently, when the plate was undisturbed, this arm rested on the floor of chamber *A*; but when an ant, ascending the incline of the plate, passed beyond the fulcrum, its weight was added to that of the shorter arm, and by the time it had come near the end of the shorter arm, the combined weight of the two

FIGURE 7.

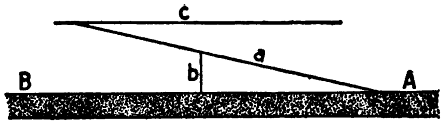


FIGURE 8.

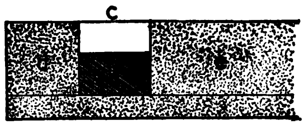


FIGURE 9.

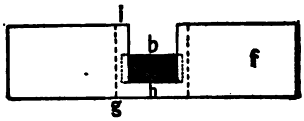


FIGURE 10.

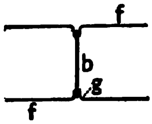
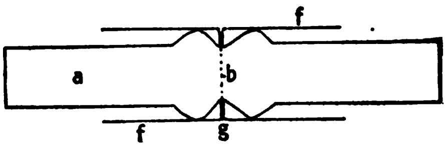


FIGURE 11.



was sufficient to tip the plate and bring the *B* end into contact with the floor. As soon as the ant had passed from the plate to the floor of chamber *B*, the weight of the long arm caused the plate to swing back into its original position. Figure 10 shows, in horizontal section, at the level of the uncovered portion of the watch spring (*b*), the fulcrum without the mica plate. As the mica plate was somewhat longer than the end of the partition, the latter was prolonged by a vertical piece of paper (*a*, *b*, Figure 6) parallel with the edge of the plate. This prevented ants from getting under the plate from the *A* side, and interfered with any attempt of a second ant to get on the *B* end of the plate while it was being held down by the weight of the ant entering *B*.

To eliminate as far as possible other factors than that of food, the latter was placed alternately in chamber *B* and in chamber *A*, the same number of observations being made for each position.

2. *Observations.* — In these experiments ten different colonies were made use of. Records in regard to the feeding activity were made every 24 hours with the exception of certain Sundays and a few holidays. It is clearly necessary, however, to exclude observations made on any day succeeding one when no observations had been made, because the time interval during which the ants had had an opportunity to respond was in such a case 48 hours instead of 24 hours, the usual interval. At the beginning of each observation the ants were all placed in chamber *A*, and the food was placed half the time in chamber *A*, half the time in chamber *B*. A "*series*" of observations consists of a number (50 or 25) of separate observations all made under the same conditions as to the relation of insects to the food-chamber. The maximum number of observations in a week was only five, except during those periods when records were made on Sundays as well as week days, in which cases *seven* observations a week were possible. During the earlier experiments on this species, 50 observations were included in each series, but later the number was reduced to 25. A "*set*" of observations includes two or more "series," one of the series being made while the food was in chamber *A*; the other while it was in *B*. The ants at the beginning of every experiment were, as stated, all in one chamber (*A*). After the lapse of 24 hours the number of individuals which had migrated into chamber *B* was noted. The results of a series of 50 (or 25) such observations were combined as follows: First was computed what per cent of the whole number of ants under observation made their way into the unoccupied chamber during each observation. These per cents for the 50 (or 25) observations were then averaged. The result is shown in Table I. When the food was in chamber *B*, these values give a partial measure of the stimulus to migration caused by food; but, assumably, the migration under this condition was not due exclusively to the stimulus of food. To eliminate as far as possible all other factors except food, experiments were also made with the food in chamber *A*. The individuals making their way from chamber *A* to chamber *B* under this condition would clearly not be attracted to *B* by food, and the number of them may fairly be taken as an approximate measure of the number of individuals which made their way into the food-chamber (when that chamber was *B*) independently of the influence of food. In the earlier sets of observations (viz. with 50 observations in a series) *three* series were combined into a set (colonies 4, 17, 20, and 24); in the later sets only *two* series (colonies

TABLE I.[1]

(24-Hour Intervals.)

Colony	4	4	4	17	17	17	20	20	20	24	24	24	42	42	51	51	52	52	53	53	54	54	55	55
Chamber containing food	B	A	B	B	A	B	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	B
No. of observations	50	50	50	50	50	50	50	50	50	50	50	50	25	25	25	25	25	25	25	25	25	25	25	25
Av. no. of workers in colony	7.6	5.3	3.3	28.3	49.5	20.2	78.9	57.7	53.1	56.6	55.9	20.6	13	10	17	12	19	9	30	21	38	27	7	5
Per cent of workers entering B (whether containing food or not)	27.1	10.6	33.8	25.4	6.8	25.7	6.7	1.2	6.5	3.2	29.2	8.9	37	17	17	22	16	23	15	38	19	3	21	38
Av. of per cent of 2 "sets" in one chamber	..	30.5	..	..	25.7	..	..	6.6	..	..	6.1	..	..	..	..	..	..	..	..	..	..	..	..	..
Av. no. of winged queens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	4	5	5	1	1	..	..
Per cent of winged queens entering B (whether containing food or not)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0	0	27	58	0	0	..	..
Av. no. of deälated queens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0	0	1	1	1	1	..	..
Per cent of deälated queens entering B (whether containing food or not)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	28	48	0	0	..	..
Av. per cent when food was in B, 21.2.													Av. per cent when food was in A, 15.6.											

[1] Owing to the death of some members of a colony, the number varied. The average number in a colony was determined by taking the sum of the individuals found in the nest on successive days and dividing that by the number of observations.

42, 51, 53, 54, 55). Usually the three-series set embraced two series with the food in B and one with the food in A, but in one instance (colony 24) the reverse was true, two series of observations having been made with food in A, and only one with food in B. These three series were so arranged as to eliminate as far as possible any tendency of the colony to a change in its activities during several weeks of observation, by putting one of the two series *before*, the other *after* the odd series. Although the results may differ considerably in different experiments, and the proportions found may be so variable as to show that we are dealing with rough approximations only, still the numerical relations are the only basis we have to go by, and are not less reliable than vague statements that there are "many" or "very many" more engaged in this than in that activity. Accordingly, I shall give the numerical results of my observations, which are of necessity the basis of my general statements of proportions.

In those cases where two series of observations were made with the food in the same chamber, it was found that there is not much difference in the per cents resulting in the two cases (27.1 and 33.8; 25.4 and 25.7; 6.7 and 6.5; 3.2 and 8.9). In experiments with colonies 4, 17, 24, 42, and 54 there was a much larger number of ants entering B when the food was in B than when it was in A, as we should expect; but, for some reason which I have been unable to explain, the reverse was true in colonies 51, 52, 53 and 55. However, the average of these per cents was higher when the food was in B (21.2 per cent) than when it was in A (15.6 per cent). This would leave a difference of 5.6 per cent, which may be assumed as the per cent which went to B for food alone. It will be noticed that the per cent of ants entering B is fairly low, showing that not every ant went each day to the food chamber, and, indeed, some ants did not enter B at all. This is shown by an examination of the details of a series of observations in colony 54. The ants whose numbers are not recorded here died before this experiment was performed. Nos. 25, 28, 35, 37, 39, 45, 47 and 48 did not enter chamber B at all, while out of a possible 33 times, No. 30 entered B twenty-two times; No. 2, twenty times; Nos. 21 and 22, seventeen times each; Nos. 10 and 12, sixteen times each; Nos. 3 and 52, fifteen times each; No. 9, eleven times; No. 20, eight times; No. 44, six times; No. 14, five times; Nos. 8 and 13, three times each; Nos. 11, 17, 19, 31, 34, and 42, twice each; and Nos. 15, 19, 33, 36, and 40, once each. There were, in fact, instances in all the colonies of failure on the part of some individuals to enter the food-chamber. It might be urged that any one individual does not need food every day, and can readily live for some time without it, as has

TABLE II.

(48-Hour Intervals.)

Colony	4	4	4	17	17	17	20	20	20	24	24	24	42	42	51	51	52	52	53	53	54	54	55	55
Chamber containing Food	B	A	B	B	A	B	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A
Av. no. of workers	8.1	:	:	52	:	16.8	84.4	:	52.4	:	45	20.7	12.8	10.2	20.4	12	23.6	9.3	31.2	20.9	39.2	27.3	7	5
Per cent of workers entering B (whether containing food or not)	36.4	:	:	34.3	:	28	6	:	4.6	:	32.7	6.2	40.4	26.2	29.2	26.4	14.4	32.7	16.7	43.9	23.8	7.7	32	52.8

Av. per cent when food was in B, 24.3.

Av. per cent when food was in A, 28.

been shown by Janet ('98) and by Fielde (: 04[b]) ; but in my experiments many individuals did not enter the food-chamber for a long period, fifty days, and while it is possible that they may exist for such a period when deprived of food, I do not believe that with food within their reach they would, as a rule, go so long without eating. Moreover, it is certain that not every individual is dependent for its food on a personal visit to the food-chamber, because I have often seen ants, immediately after being taken from *B* (containing food) and placed back in *A*, regurgitate food to their fellows, so that the failure of a particular ant to visit the food-chamber by no means warrants the conclusion that it has remained without nutrition. Many of the nests contained queens, males, and larvae, all of which throve, the ants being able to rear their young in chamber *A* provided proper food was kept in *B*, and provided the ants which entered *B* were placed back in *A*. Colony 4 was the only one without a queen, but as the ants even in this colony flourished, it cannot be said that in all cases the food is supplied by queens, either through their fat-bodies or otherwise as is done when a queen is founding a colony.

Table II was made up in exactly the same manner as Table I, except that the intervals between observations were 48 hours instead of 24. In the cases of colonies 24, 42, 51, and 54, the per cents of ants entering *B* were larger when the food was in *B* than when it was in *A* ; the reverse was true in colonies 52, 53, and 55. The deficiencies in the records of colonies 4, 17, 20, and 24 are due to the fact that these colonies were examined

every 24 hours, during at least one series when the food was in *A* or in *B*. A comparison of the results of these two tables shows that there is one colony (51) from which during the 24-hour periods more ants entered *B* when the food was in *A* than when it was in *B*; but which in the 48-hour periods gave the opposite result. All those colonies which in the 24-hour periods showed more ants entering *B* when the food was in *B* than when it was in *A*, showed the same results in the 48-hour periods. In the 48-hour periods, as in the 24-hour periods, when there was more than one series with food in *B*, the per cents of ants in *B* were fairly similar in the two cases (34.3 and 28; 6 and 4.6), nor are the results very different in a given colony (17 and 20) for the 24- and 48-hour periods. On the whole, when we compare the results in the 24-hour periods and the 48-hour periods, it will be seen that there were somewhat more ants entering *B* during the 48-hour periods than during the 24-hour periods. In the 48-hour periods there were rather more ants entering *B* when the food was in *A* than when it was in *B*, as opposed to the reverse condition shown for the 24-hour periods. I believe this to be due to the fact that there were several colonies (4, 17, 20, and 24) which, throughout one or more series, were examined daily (consequently no 48-hour periods) and these were colonies which, during the 24-hour periods showed more ants entering *B* when the food was in *B*.

To ascertain the constancy of individuals in regard to foraging, I noted the number of times which each ant had the opportunity (one opportunity in 24 hours) to go into *B*, and also the number of times which it availed itself of this opportunity. From the ratio of the two numbers, expressed in per cents, was subtracted a similar ratio ascertained when the food was in *A*, since we must assume that the ants entering *B* when the food was in *A* did so for some other purpose than that of obtaining food, and that an equal number would presumably have passed from *A* to *B* when the food was in *B* for similar reasons, i. e. *not* for food. These results are given in Table III, where the second column shows the number of ants engaged in foraging for each of the several per cents from −78 to 85. For the sake of convenience the results of the corresponding operation for the activities of tending the young (third column) and building (fourth column) are incorporated in the same table. The results on foraging would have been more convincing had more ants in all colonies entered *B* when the food was in *B* than when it was in *A*. But as has been stated, it was frequently found that an individual ant entered *B* more often when the food was in *A* than when it was in *B*.

In compiling Table III, I have disregarded in respect to every activity all individuals which died before the end of the experiment. There

were many ants which did not engage in foraging at all (76 out of 195, or about 39 per cent), while only a few entered B a large part of the possible number of times — only 8 out of 195, for example, taking advantage of more than half their opportunities. This suggests some sort of division of labor, and thus agrees with Lubbock's ('82) observations, although the number of individuals which constantly engaged in this activity was much larger in my studies than in his. This difference may have been due in part to our having used different species of ants, but also in part to differences in our methods of experiment-

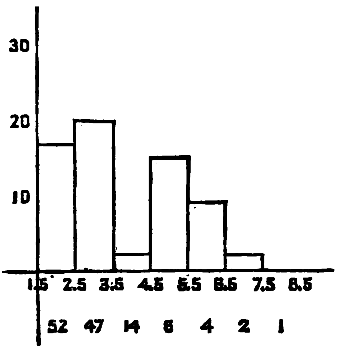


FIGURE 12.
(Foraging.)

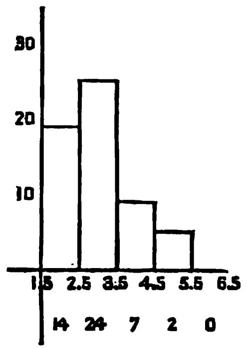


FIGURE 13.
(Tending the Young.)

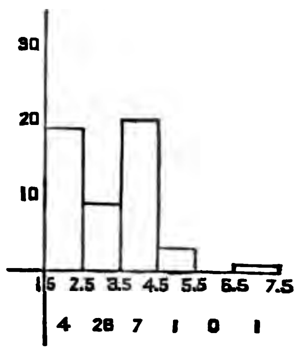


FIGURE 14.
(Building.)

ing and observing. His ants had perfect freedom to go to and from the food, being therefore able immediately to return with food to their fellows; whereas mine had to wait for a longer or shorter time before returning, in some cases probably nearly twenty-four hours, with the result that those of my ants which entered the food-chamber were for much of the time of no use as a source of food supply to the rest of the colony, in consequence of which other ants probably went in search of food, making the total number of food-seekers somewhat larger than it would have been but for this restraint. His observations of unrestrained ants were made once an hour; mine, made on ants that were free to enter the food chamber, but could not leave it, were made only once a day. However, I do not think this wholly explains matters, for on days immediately following those on which no record had been taken, there were not many more foraging ants than after an interval of only twenty-four hours, which seems to me to show that nearly all individuals likely to frequent the food-chamber had done so during the first twenty-four hours. Moreover, the artificial heating of my ants

may have had something to do with the difference in our results, for while my ants were thus stimulated to unusual activity, his experiments were carried on at room temperature in winter.

TABLE III.

Given %.	Foraging.	Tending Young.	Building.	Given %.	Foraging.	Tending Young.	Building.	Given %.	Foraging.	Tending Young.	Building.	Given %.	Foraging.	Tending Young.	Building.	Given %.	Foraging.	Tending Young.	Building.	
−78	1	..	..	−44	..	..	..	−10	1	..	..	24	1	1	..	58	1	..	..	
−77	..	..	..	−43	..	..	..	− 9	1	..	..	25	1	..	1	59	..	..	1	
−76	..	..	..	−42	..	..	..	− 8	..	..	..	26	1	2	..	60	..	1	..	
−75	..	..	..	−41	..	..	..	− 7	2	..	..	27	..	..	..	61	1	..	..	
−74	..	..	..	−40	..	..	..	− 6	..	..	..	28	2	1	..	62	..	..	..	
−73	..	..	..	−39	..	..	..	− 5	..	..	..	29	1	..	1	63	..	..	..	
−72	..	..	..	−38	..	..	..	− 4	3	..	..	30	1	3	..	64	..	..	..	
−71	1	..	..	−37	..	..	..	− 3	1	..	..	31	1	..	..	65	..	..	..	
−70	..	..	..	−36	1	..	..	− 2	1	..	..	32	..	2	..	66	..	..	..	
−69	..	..	..	−35	1	..	..	− 1	..	..	..	33	2	..	..	67	..	..	..	
−68	..	..	..	−34	..	..	..	0	76	7	5	34	..	1	..	68	..	..	..	
−67	..	..	..	−33	..	..	..	1	..	..	4	35	1	..	1	69	..	..	..	
−66	..	..	..	−32	..	..	..	2	20	2	5	36	2	1	..	70	..	..	..	
−65	1	..	..	−31	..	..	..	3	9	..	3	37	..	..	..	71	..	..	..	
−64	1	..	..	−30	1	..	..	4	2	2	2	38	1	1	..	72	..	..	..	
−63	..	..	..	−29	1	..	..	5	3	..	1	39	..	..	..	73	..	..	..	
−62	..	..	..	−28	..	..	..	6	6	4	1	40	1	1	..	74	1	1	..	
−61	1	..	..	−27	..	..	..	7	5	..	3	41	..	..	..	75	..	..	..	
−60	..	..	..	−26	1	..	..	8	..	2	1	42	..	..	..	76	..	..	..	
−59	..	..	..	−25	..	..	..	9	5	..	1	43	..	..	..	77	..	..	..	
−58	..	..	..	−24	..	..	..	10	..	3	1	44	..	..	1	78	..	..	..	
−57	1	..	..	−23	..	..	..	11	2	..	2	45	..	..	..	79	1	..	..	
−56	..	..	..	−22	..	..	..	12	..	2	1	46	3	1	..	80	..	..	..	
−55	1	..	..	−21	..	..	..	13	..	..	..	47	..	..	1	81	..	..	..	
−54	..	..	..	−20	1	..	..	14	1	1	1	48	..	..	..	82	1	..	..	
−53	..	..	..	−19	2	..	..	15	4	..	1	49	..	..	..	83	..	..	..	
−52	..	..	..	−18	..	..	..	16	..	1	1	50	..	2	..	84	..	..	..	
−51	..	..	..	−17	..	..	..	17	..	..	..	51	1	..	..	85	1	..	..	
−50	..	..	..	−16	..	..	..	18	3	2	1	52	..	..	..	..	195	46	43	Total no. ants engaged in each activity
−49	..	..	..	−15	..	..	..	19	1	..	..	53	..	..	..	..	92	39	38	No. reacting positively
−48	..	..	..	−14	..	..	..	20	..	..	..	54	..	1	..	..	27	0	0	No. reacting negatively
−47	..	..	..	−13	1	..	..	21	2	..	..	55	..	..	..	..	76	7	5	No. not reacting
−46	..	..	..	−12	..	..	..	22	..	..	2	56	..	..	..	..	8	5	1	No. reacting positively more than 50 per cent
−45	1	..	..	−11	..	..	..	23	3	1	1	57	1	..	..	..	..	..	..	

I do not find from these experiments any very striking evidence of a correlation between size and the habit of foraging. I have plotted frequency polygons (Figures 12–14) for three of the various activities studied. For this purpose the ants experimented with were divided into six classes, based on the size of the head expressed in sq. mm. (length × breadth). The class values are indicated along the axis of abcissas. The values along the axis of ordinates are the average per

cent of times (the opportunities being 100 per cent) which ants of these sizes entered into the activities of foraging (Figure 12), tending the young (Figure 13), and building (Figure 14), respectively. The figures below the middle of each class show the number of individuals in that class. There seems to be no marked difference as to the amount of foraging among the various classes, except that the largest ants did not engage much in that activity. It might be objected that the colonies should not have been classed together in this way, since there might be differences in behavior of the classes of different colonies, depending on the number of ants of each size within the colony, numbers which change with the age and amount of food of the colony. But here the colonies, being all small, were in approximately the same condition, and were kept in the same environment. Moreover, such a combining of colonies would tend not to exaggerate but to obliterate differences in behavior of the different classes, and yet such differences are more or less evident.

2. *Tending the Young.*

1. *Methods.* — In endeavoring to ascertain which ants were most active in tending the young, both passages at the ends of the partition in the Fielde nest were left open. The ants were placed in chamber *A*, and this was left partially darkened until the ants had collected in the darkest part of the chamber. Then the screen was removed, allowing the daylight to fall upon the insects. In order to cause ants more quickly to pick up the young, a gentle current of air was pumped into the corner of the nest where the ants were congregated. The pumping was done by the following method: A five-gallon glass carboy was used as a compression chamber for the air. Into this the air was pumped by means of a foot-bellows, connected to the carboy by a heavy rubber tube. Another tube leading from the carboy terminated in a piece of glass tubing drawn out to a fine point, which was inserted through a small hole in one of the two roof-panes of the nest.

Four colonies were used in this experiment. Each colony was observed for 50 one-minute periods. During each period a record was made of all ants seen carrying eggs or larvae (there were no pupae). The average number [2] of workers in each colony was then found (Table IV, line 3) and finally the per cent of workers which were active in tending the young (line 4). In a similar manner, line 5 gives the average number of winged queens in the colony, line 7 the average

[2] See page 450, foot-note 1.

number of deälated queens, and lines 6 and 8 the per cent of times that these were respectively active in tending the young.

2. *Observations.* — I may note here the following incidental observations:

(1) Ants often appeared to touch the young, even with the antennae, without seeming to notice them.

(2) Unless violently disturbed, the ants did not remove the young to a definitely safe place, but wandered about with them in their mouths in an apparently aimless way.

(3) After an experiment had continued for some minutes, the ants were not as much disturbed by the current of air as they were at first.

TABLE IV.

No. of the Colony	42	51	54	55
No. of observations	50	50	50	50
Av. no. of workers in colony	5	10	23	24
Per cent of workers tending young	17	8	31	9
Av. no. of winged queens in colony	..	2	1	..
Per cent winged queens tending young	..	0	2	..
Av. no. of deälated queens in colony	..	1	1	1
Per cent deälated queens tending young	..	0	10	2

This is in agreement with Turner's (:**07**, p. 408) statement in regard to sound, and Fielde's (:**03**[b], p. 493) in regard to other stimuli.

Unfortunately the number of individuals in a colony in this experiment was small. However, it was found (Table IV) that only a small per cent (17, 8, 31, 9) of the workers were occupied in tending the young. The per cent of workers engaged in this activity seems to be quite independent of the number of individuals in a colony.

A similar conclusion to that reached in regard to foraging (pp. 453–455), — viz. that a few individuals are more active than the rest, — is also to be drawn from my experiments on tending the young, as shown in the third column of Table III (p. 455). The methods used in experimenting allow no minus results in this activity, or in building (column 4), such as were found in foraging. Out of 46 indviduals experimented with, 7 did not share at all in tending the young, and

only 5 reacted more than half the time. On the whole, this resembles the results obtained in regard to foraging.

Figure 13 (p. 454), constructed as described on pages 455 and 456, seems to show that there is a somewhat greater activity on the part of the smaller individuals. So far as these observations go, this might be considered, as in certain aspects of foraging (pp. 453–455), to be due to a great alertness of some individuals in more than one activity, which certainly exists, and will be discussed later (pp. 462–463); but in corroboration of field experiments on *C. pictus* (pp. 468–469), it also seems to me to point clearly to a greater activity on the part of the smallest ants of *C. americanus* in tending the young.

FIGURE 15.

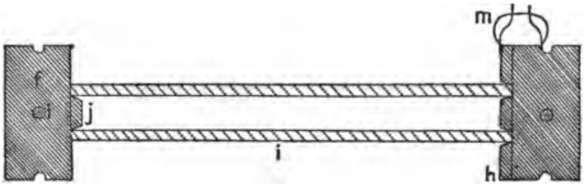
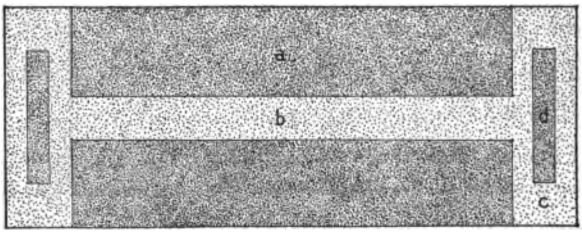


FIGURE 16.



It is somewhat peculiar that both deälated and even winged queens, as well as workers, took part in this activity.

3. *Building.*

1. *Methods.* — (*a*) *Horizontal nest.* Two kinds of nest were used in investigating this part of the problem. The first was a Fielde nest, such as was used in previously described experiments. In one chamber, kept dark except during observations, was placed damp earth, collected with the ants, so as to be of an appropriate sort. The nest was nearly filled with the earth, only enough room being left to enable the ants to walk comfortably between the earth and the roof. The other chamber was exposed to daylight and contained the food. I call this the horizontal nest.

(*b*) *Vertical nest.* The second kind of nest (Figures 15–17) was vertical, and consisted of a plaster-of-Paris base, two end pieces of wood let into two sockets (Figure 16, *d*) in the base, two sides of glass, and a wooden cover. The base (Figure 16) was 6½ inches long, 2½ inches wide, and ⅝ inch thick. The thickness of the base was increased above the level at *a* 1⅛ inches at the ends (*c*) and along the middle of its

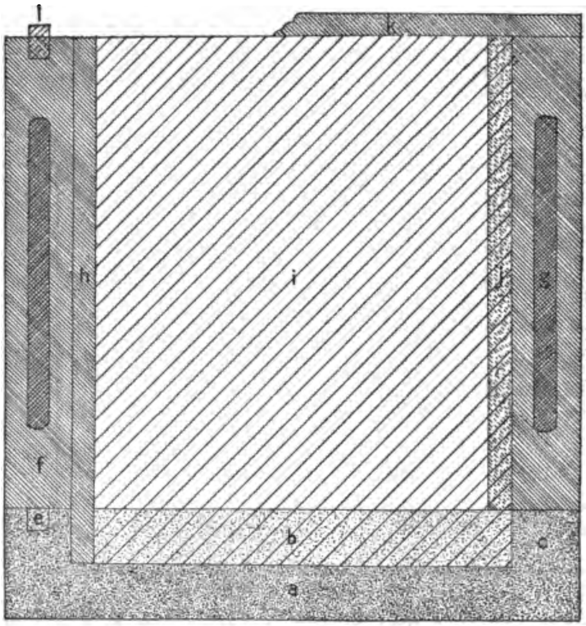


FIGURE 17.

upper surface (*b*). In each end thickening (*c*) there was a groove, or elongated mortise (*d*), which received the tenon (*e*, Figure 17) of the lower end of the wooden end piece. In the upper end of each of these pieces was inserted a cylindrical glass peg, *l* (Figure 17), to hold in place the wooden cover, *k*, which had bored in it holes corresponding in size to the peg and in such positions as to hold the end pieces parallel to each other. The end pieces were 5½ inches long, 1½ inches wide and 11/16 inch thick. To the inner surface of each was securely fastened a strip of wood (*j*) 3/16 inch thick and as wide (½ inch) as the median thickening (*b*) of the base. This strip of wood and the thickening (*b*) of the base served as stops to keep apart the two glass plates (*i*, Fig-

ure 15), 5 inches × 6 inches, which formed the sides of the chamber. When one of the glass sides had been firmly pressed against the median "stops," the two wooden strips (*h*, Figures 17, 15) were pressed against the pane and clamped in position by steel clamps (*m*, Figure 15), one jaw of which rested in a vertical groove (*g*, Figure 17) cut in the edge of the end piece, as shown in section at *m* (Figure 15). When both panes were thus clamped in position, a fairly tight chamber ½ inch thick and 5 inches × 6 inches in area was completed. This was nearly filled with earth. All wooden pieces were infiltrated with paraffin to prevent warping, as the base of the nest was occasionally placed in water to keep the

TABLE V.

No. of the Colony	54	54	53	53	52	51	51	42	42
Kind of Nest	H	V	H	V	V	H	V	H	V
No. of observations	150	150	150	150	150	150	150	150	150
Av. no. of workers in colony	22	21	17	17	2	9	5	4	2
Per cent of workers building	5	13	5	14	59	17	15	13	38
Av. no. of winged queens in colony	1	1	4	3	1	1	1	5	4
Per cent of winged queens building	0	0	4	0	3	65	0	2	0
Av. no. deälated queens in colony	1	1	2	3	1	1	2	5	6
Per cent deälated queens building	0	3	0	0	7	0	8	3	4

earth damp. In case either pane of glass needed cleaning, the nest was laid on its side with that pane uppermost, and the plate was then exchanged for a clean one by unclamping the wooden strips of that side.

2. *Observations.* — The colonies observed in this activity were especially small, so that it is not safe, perhaps, to lay much stress on the results, except in relation to other work on this subject. I give them, therefore, merely as additional evidence.

From these experiments (Table V) [3] I found, again, that the per cent of individuals engaged in this activity is, as a rule, small, and is independent of the number of individuals present in the nest. In most cases (colonies 54, 53, and 42) the per cent was smaller in the

[3] Table V was constructed in substantially the same manner as Table IV (p. 457).

horizontal nest (*H*), but in colony 51 it was smaller in the vertical (*V*). For my problem, however, this is unimportant.

In Table III, column 4, it may be noted that out of 43 ants tested in building, five did not engage at all, while only one reacted more than half the time, the largest per cent being 59. As in tending the young, the methods employed allow only positive results.

Figure 14 (p. 454) shows a distinct correlation between size of the individual and activity. It will be noticed that this activity is almost confined to the smaller sizes (1.5 mm.–4.5 mm.).

TABLE VI.

Classes,		1		2		3		4	
		1.40–3.19 sq. mm.		3.20–4.99 sq. mm.		5.00–6.79 sq. mm.		6.80–8.59 sq. mm.	
No. of Colony.	No. of observations.	No. of Individuals.	Per cent active.	No. of Individuals.	Per cent active.	No. of Individuals.	Per cent active.	No. of Individuals.	Per cent active.
90	50	2	29	2	28	2	26	2	30
89	50	10	20	10	18	10	17	10	32

But here again, as in tending the young, both deälated and winged queens took part.

4. *Fighting.*

1. *Methods.* — It was impracticable to deal here with the colony as a whole, since it was impossible in the confusion which occurred to distinguish readily the sizes which took part. In order to discover which of four different known sizes (classes) was more active in fighting, a few individuals of each size were placed in four separate Stender dishes, one dish for each size. Each dish measured 5.5 cm. in diameter and contained the same number (given in Table VI) of ants. The limits of the head sizes of the individuals in each of the four classes is indicated in sq. mm. Into each dish in succession was introduced

for a period of thirty seconds a worker from another colony of *Camponotus americanus*, and the number of ants attacking it was noted for each dish.

2. *Observations.* — Table VI gives the results of these experiments. The first column gives the number of the colony, the second the number of observations made on each colony. The results for each of the four classes of ants are shown separately; for each class the first column shows the whole number of individuals of that class under observation, the second column the per cent of activity.[4]

Two colonies were observed in these experiments, and in both cases it was found that the largest size took part slightly more often than the other sizes. They were, too, more savage in their attacks. For the first time, then, we seem to have an indication of greater activity on the part of the large workers. This might, of course, be due to differences in surrounding conditions, for in the other activities Fielde nests were used (pp. 446, 456, 458), and in fighting, Stender dishes; but in view of work done in the field on *Camponotus pictus* (pp. 468–471), I hardly think that this is the explanation. It seems to me, rather, that it is due to division of labor, though here, again, the distinction is not hard and fast, as all sizes are very active, but the largest workers most so.

5. *Relations of Classes to Various Activities.*

Having discussed foraging, tending the young, building, and fighting in their various aspects, attention should now be directed to the specific question of the relation between size and the various activities. If we examine Figures 12–14 we see that, while the correlation between the size of the ants and the three first mentioned activities is not in all cases striking, nevertheless, on the whole, the smaller ants are the more active in each of these functions. This is even more evident when the curves given in Figures 12–14 are combined (Figure 18) so as to show the total activity for these three occupations for each size. In the case of fighting, on the contrary, it is the larger individuals which show the greater activity.

It is another question whether a *given individual* shares in all activities, for it is conceivable that certain individuals of a given size-class confine their attention to one mode, and others of the same size-class exhibit theirs in another mode of performance. As a matter of fact, I

[4] The per cent active was found in each case by first ascertaining the number of ants active during each observation; the per cent which this number was of the whole number of ants in a given dish was then found, and finally these per cents were averaged for each dish from each colony.

have frequently seen the same ant occupied first in one and then in another activity. Indeed, some individuals were about equally concerned in two or more activities. When, however, we consider all the evidence on the various activities, we are warranted in the conclusion that in fighting, the largest ants predominate; in building, the small and middle-sized ones; in tending the young, the smaller individuals; and in foraging, all sizes except the largest. From field evidence on *Camponotus pictus* I can corroborate these conclusions.

And yet it is evident that certain individuals, regardless of size, are much more alert in each activity than others; this at first sight suggests a division of labor not correlated with size differences. In Figure 19 individual ants, arranged on the axis of abcissas in the order of the size of the head, are designated by the letters of the alphabet; at the left the ordinates indicate the per cents of the possible number of times which each of these twenty-one individuals ($A-U$) was engaged in the several activities, these being plotted as solid black lines. The upper curve shows "building," the second, "tending the young," the third, "foraging," and the fourth (bottom) is the sum of the other three curves, which thus gives the total activity of each individual for these three occupations.

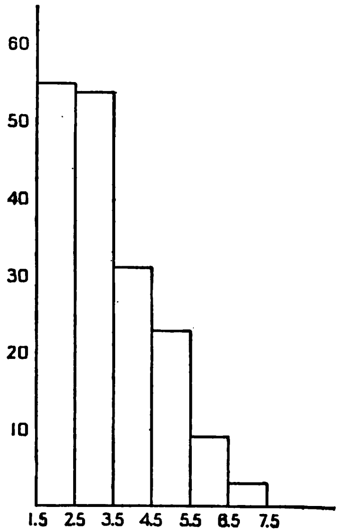


FIGURE 18.

The dotted curve shows the various head sizes in sq. mm. (length × width), the values being indicated by the figures in the right margin. It may be seen at a glance: (1) that there is no very obvious correlation between any of the activities when compared with one another (curves 1, 2, and 3); (2) that there is no close correlation between any of the various activities and the size of the head (compare curves 1, 2, and 3 with the dotted curve); and (3) that certain individuals are in general much more active than others (bottom curve). The fourth curve shows that, on the whole, the smaller individuals are the more active. While there is a slight preponderance of certain sizes (D = 2.30 sq. mm.) in certain activities (building), there is also an individual diligence in several activities, and this seems to be more or less independent of size.

In regard to the behavior of queens, it may be said that it was only rarely that they shared in any of the activities described above, and then it was usually under more or less exciting influences. This activity was, in all probability, a reversion in the case of deälated individuals to the condition of the queen when founding a colony, and in the cases of winged individuals to the condition in the parental nest (see Wheeler, :06[a]).

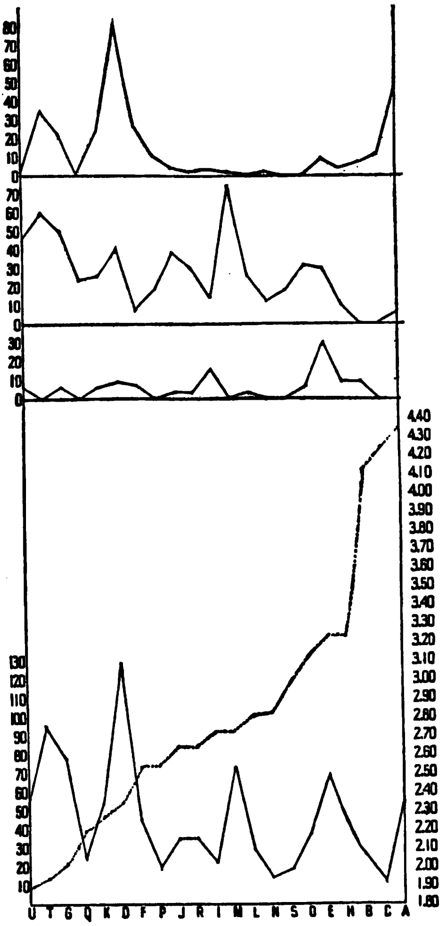


Figure 19.

6. *Conclusions in Regard to Camponotus americanus.*

From the foregoing account it appears that:

1. Males were never active in the duties of the nest.

2. The proportion of workers occupied in any given activity seems to be independent of the number of individuals in the colony, when the colony is as small as those here studied.

3. Queens, even when retaining their wings, may take part in certain activities in small colonies, although the colony has reached such an age as to contain all classes.

4. A few individuals are very constant in a certain activity, or in even more than one, the majority being much less active.

5. Some individuals are about equally concerned in two or more activities.

6. Too few individuals were available in making up Figures 12–14 to show division of labor as clearly for this species as is seen in *C. pictus*

when examined in the field (pp. 467–471). There seems here to be a greater activity on the part of some individuals than of others, irrespective of size; this is probably due to psychological differences of individuals, as suggested by Escherich (:06, p. 45). But there seems also to be some evidence of a division of labor correlated with polymorphism; this is not marked by hard and fast lines, since all classes may share in any activity, but by a *preponderance* (*a*) of large ants in fighting, (*b*) of those of medium and small size in building, (*c*) of those of small size in tending the young, and (*d*) of those of small and medium size in foraging.

7. The small and medium-sized workers are, in general, much more active than the largest ones.

B. Camponotus herculeanus pictus.

i. In Barth Nests.

1. *Methods.* — In Barth nests, 8 inches high × 6 inches in diameter, with ¾ inch between the jars, five colonies of *C. herculeanus pictus* were studied, all of which had been previously studied in the field, the object being to compare the two sets of studies with a view to learning if the ants behaved differently in the laboratory from what they did in the field. In other words, the field studies afforded a control for those in the laboratory. Therefore, not only those activities which had been unsatisfactorily examined in the field were studied, but also all others. The colonies were necessarily smaller than those in the natural nests, as it was impossible to collect the whole of a colony. I attribute to this diminution of the size of the colony the fact that, as a whole, the ants in captivity were less active than those in the field, for it will later be seen (p. 471) that in the normal state the smaller colonies of *Camponotus herculeanus pictus* were less active than the larger.

2. *Observations.* — In the Barth nests I have never seen any of these ants carrying in food, *feeding* themselves, or preparing food. More of the intermediate sizes than of any other size were seen outside of the earth at the top of the nest, or running about in the bottom of the well, i. e. the inside jar, a condition which may be compared to foraging. The other two sizes about equalled each other in this activity.

In *regurgitating* and receiving regurgitated food it is difficult to see in which direction the food passes. But as I have seen this process occur between all possible combinations of majors, intermediates, and minors, no one class can be the sole regurgitators; I rather suspect that it is more common for the two smaller classes to regurgitate, and for the majors to receive. The reasons are as follows: First, the

majors were several times seen drumming on the heads of these two classes, both immediately before this activity took place and during its performance, whereas this drumming was never seen in the other two classes. Apparently the same stimulus is used by ants to make aphids give out secretions (Forel, '74, p. 251) and to make ants regurgitate (l. c., p. 243. See also Wheeler, :01[c], p. 438). This leads me to think that it is the ant desiring food, rather than the one giving it, which does this tapping. Secondly, throughout all my observations on this species and *C. americanus*, it is the class of large ants which has less to do with collecting food than the other classes. Thirdly, the large ants are, on the whole, so much more lazy than the intermediates and minors that it is characteristic for them to take food which is easily obtained from other ants near at hand rather than to seek it or prepare it for themselves. Of course they probably do often obtain other food, and the other classes certainly sometimes receive regurgitated food; but for the reasons stated, I am inclined to think that in general the majors are more apt to receive regurgitated food, the intermediates and minors to give it. On one occasion I saw an intermediate and a queen, on another a minor and a queen engaged in regurgitation, but I am unable to say which way the food went during the process.

In *licking*, all three classes took part, but the majors slightly less often. The majors were never licked, and the minors seldom, the intermediates being most often the objects of this activity. There were not many individuals, however, which shared in this activity, so that this evidence may not have great weight by itself; it may, however, help to confirm other evidence.

Practically the same conditions in regard to *tending the young* hold true here as in the same colonies out of doors, viz. that there are many minors, few intermediates and no majors so engaged. This was particularly noticeable in colony R 18, where the nest consisted of two chambers, an upper and a lower, with a short gallery connecting the two, and another gallery leading to the surface. It was a marked fact that day after day the large and some of the intermediate ants stayed in the lower chamber, while the other intermediates and all the small ants were in the upper chamber with the larvae. Moreover, when the ants were stimulated with the heat from the electric bulb (pp. 440–443), it was nearly always the small ants which carried the larvae toward the heat, or away from it when it was too great. In regard to the chambers and galleries, I have noticed both here and in out-of-door colonies that ants do not, as a rule, collect in the galleries, but use these rather as passages; they are inclined to huddle together in the chambers.

In *building*, both in digging and in carrying earth, it was the majors

and intermediates which performed the greater part, the minors hardly sharing at all. Digging is here similar to that described for *Pheidole pilifera* (p. 485).

Carrying (and being carried) was not a frequent occurrence, and even when it did occur, it was, in these nests, rather a dragging than a carrying. In the few cases where it was observed, minors were dragging intermediates or majors, and no minors were dragged.

Any unemployed ants may collect in the chamber with the queen, regardless of their size, and I have no reason to think that one size is more apt to do this than is another.

When the nest is jarred, or the earth on top broken, ants of all sizes become much excited. Here there did not seem to be a difference in the reaction of ants of different sizes as there was in the out-door nests.

Nothing resembling guarding was observed.

ii. In Out-door Nests.

1. *Field Notes.*

1. *Methods.* — In considering these notes it should be remembered that the records were made at the time the ants were captured, and therefore before any conclusions could have been deduced from them. Later, the ants were arranged in series, and they will be described further on (pp. 469–471). The results of these field observations are of course additional to those obtained by actually collecting and arranging other ants in series. So far as they agree with the results deduced from collected material (see pp. 469–471), they strengthen the conclusions drawn from that material. The classes had to be determined arbitrarily, and were designated as "majors," "intermediates," and "minors." The numbers were also, as a rule, only approximate, and were classed as "many," "some," and "few," except where actual numbers are given, when they always fell under "few." The approximate numbers of individuals of each class occupied each day in each activity, then, were observed, and a summary was made first for each colony, and later a summary for all the colonies taken together. The lack of records in several of these activities (regurgitating and receiving regurgitated food, licking and being licked, and as a rule, surrounding the queen) is due to the fact that it is difficult, and often impossible, to observe them in an undisturbed out-door nest, and one must therefore depend upon as natural conditions as possible in the laboratory to show facts concerning them. Though digging is not represented here, nevertheless I succeeded in capturing ants engaged in this activity

(p. 469). Fighting is probably partially represented by "disturbed by knocking."

2. *Observations.* — In the out-door work on *Camponotus herculeanus pictus* it was evident that many more ants, probably even a greater proportion of the colony, took part in the various activities than was the case with *Camponotus americanus* in the laboratory; and yet, when compared with the total population, it was noticeable that few were engaged in any kind of work at one time. This was best seen in foraging; for no matter how many ants were in the field, when the nest was opened a vastly greater number of individuals was revealed within.

In regard to those activities which were successfully observed in the field, it was found that the intermediates and minors take a much more active part than do the majors, and on the whole, the intermediates are here slightly more active than the minors.

Except for those ants which were captured, only two, an intermediate and a major, were seen actually carrying in food.

The majors were least active in "tending the young," the intermediates more active, and the minors most so.

As for building, all sizes were seen carrying earth, though the two smaller sizes excelled in this, especially the minors. No ants were observed digging, except those which were captured.

The act of carrying I think is most frequently manifested when the ants are somewhat excited, either by some disturbance or by the presence of food. This activity is on the whole not very common, but in these out-of-door nests, the process seems to be one of actually carrying rather than of dragging, which was observed in the Barth nests (p. 467).

My impression is very strong that, while all classes are disturbed when the nest is knocked upon or broken into, and while all will attack an intruder vigorously, it is on the whole the majors in this species which exhibit most zest in this response. They gnash their jaws, curl their abdomens forward under the rest of the body in order to throw poison on the enemy, and appear very savage. If they once get hold of an enemy, they cling with bull-dog tenacity, keeping a firm grip with their mandibles even after death. While all this is also true to some extent of the intermediates and the minors, it is the majors which are the fiercest.

The note-book evidence, then, seems to show that the minors are the most active in tending the young, somewhat larger ants in foraging and in building, and that the majors are more or less reserved for fighting. There is, however, no hard and fast division between classes

either morphologically or physiologically, and therefore, all that one can say is that ants of certain sizes predominate in a given activity.

Another very striking conclusion which may be drawn from the field notes is that on the whole the majors are relatively inactive in all occupations except fighting, while the other two sizes taken together are very active. Only a small proportion of the colony is at one time occupied in any given activity.

2. *Captured Ants.*

1. *Methods.* — Ants of twenty-two colonies of *Camponotus herculeanus pictus* were studied in their natural out-door nests, as described on pages 467–469. When insects from the same nests had been killed, they were, as mounted specimens, arranged in series according to size, and a permanent record of each series was secured by means of photographs showing the insects' natural size. This was done to show particular facts given below. One series consisted of ants engaged in foraging (*a*, all the ants seen in the field; *b*, ants seen carrying food in the field); a second, tending the young; a third, building (*a*, carrying earth; *b*, digging; *c*, digging under excitement); a fourth, surrounding the queen; a fifth, carrying other ants; a sixth, being carried by other ants; a seventh, fighting, i. e. rushing out when the nest was disturbed, or running about excitedly five minutes after the nest had been disturbed. In order to compare the various colonies studied for each activity, the ants of each colony engaged in a given activity were arranged by themselves, according to size, from the smallest to the largest. Other series were also made, where no attention was paid to colonies, all the ants taking part in each occupation being arranged in a single series.

2. *Observations.* — In the case of each occupation it was found that there was a perfectly graded series of sizes, i. e. with no division into classes; this means that all sizes take part in each activity which was tested. This was especially marked when all the colonies were arranged in a single series.

But when the various occupations were compared with one another, it was found that, although ants of various sizes shared in each activity, in some activities there is much more of a tendency for the large ants to take part, while the smaller ants are more inclined to share in other activities. The smaller ants, for example, are much more apt to tend the young, while the larger ones are more prone to rush out when the nest is disturbed. Thus, I was able to group the series representing the several activities in such a way that the series in which the small ants predominated were at one end, and those in which the

large predominated at the other. The several series fell into the following order, beginning with those in which the smallest sizes predominated: (1) tending the young, (2) foraging, including ants actually carrying food, — which was done neither by the very large nor the very small, — (3) surrounding a very young queen, carrying other ants, and being carried by other ants (the ants in these series being of about equal size), (4) building, (5) responding to external disturbances. It should be stated, however, that the three activities listed under 3, as well as that of actually carrying food, had only a few individuals in each. Of the other activities, tending the young was exhibited by 114 individuals, foraging by 96, building by 42, and responding to disturbances by 56. A series was also made of 74 individuals which were tending the young under excitement, i. e. when their nests were disturbed; these ants were, on the whole, much larger than those which were collected under normal conditions of tending the young. To watch this activity under normal conditions is more difficult than to watch several of the other activities; but in some colonies the ants brought the young near openings in the nests, or in carrying them from one part of the nest to another, had to pass exposed places, so that I was thus able to observe and capture them. I was also able on some occasions to open the nest suddenly enough to see ants tending the young before they became disturbed. Although from the shape of the heads of all sizes of individuals one would not expect to find any specialized guards, such as are found in Colobopsis (Lubbock, '**82**; Forel, '**74**; :**03**, p. 83; :**05**, pp. 453–454; Escherich, :**06**, p. 46; Wheeler, :**04**[a], :**10**, pp. 184, 211–212), nevertheless I made an examination to see if there were any indication that special guards existed. This species does not appear to guard the entrances in any way, but, with the exception of those individuals which are going in and out, all individuals are more apt to stay quietly huddled together in chambers within the nest. By trimming off little by little the decayed wood of the nest, along the passages, working from the outside in, and taking great care to create no disturbance, I have succeeded in making this observation repeatedly. No queens were engaged in any of the activities, probably because here there were a sufficient number of workers to attend to the needs of the colony.

In order to see how much influence the size of the colony had on the sort of individuals participating in certain occupations, I noted, at the time the ants were collected, the size of the colony. This had to be estimated roughly, and when statements of the size of a given colony were recorded on different days, these separate estimates were considered in making up the final estimate; colonies were classed as very

large, large, small, and very small, but none of them were so small as those of *C. americanus*, which had been previously used. The mounted ants, arranged in series for each occupation according to colonies, were then compared colony with colony, keeping in mind the size of the original out-door colony from which they were captured. It was found that in regard to foraging, the sorts of individuals were practically the same, irrespective of the size of the colony. There was, however, this difference in behavior, that the large colonies sent proportionately more workers into the field, probably because large colonies are apt to be less timid than small ones. Forel ('**74**, p. 249) has also noticed this fact.

While also proportionally more ants were active in tending the young in the large colonies, I failed to find any correlation between the *size* of the workers engaged in this activity and the numbers in the colony. In tending the young under excitement and in responding to disturbances, there were hardly any ants from small colonies, so that a comparison between large and small colonies could not be made for these activities. So few ants were seen bringing in food that it was impossible to ascertain whether such correlation exists in that activity or not. As it does not, however, exist in ants seen in the field, when those without food are considered together, it is highly probable that it is also wanting here. In carrying other ants, in being carried by other ants, and in carrying earth, no correlation was found.

Of course it must be remembered that, — as Wheeler (:**02**) found in Pheidole and Pricer (:**08**) in certain species of Camponotus, — in colonies which are extremely small because of poor nourishment, due to the youth of the colony or to other causes, there are no large workers, or at most only a few, and hence all the duties must be performed by the small ants. My remarks in regard to lack of correlation between the size of the colony and the sorts of ants engaged in various activities would therefore apply only to such colonies as have all the sizes which are normal to them. Also, there are, in proportion to the whole number of active ants, rather fewer large ants engaged in most of the activities in these wild colonies than in the small colonies in artificial nests described above.

iii. Correlation between Age and Function.

1. *Methods.* — When an ant emerges from the pupal state it is very light in color, but begins almost immediately to grow darker, taking, according to the species, a longer or shorter time to reach its ultimate color tone. McCook ('**79**, p. 20), Forel ('**74**, p. 262), Pérez (:**00**, p. 769), and Moreno (:**00**) claim that ants, when they first emerge, do not go out or fight, but attend to duties within the nest. That there is some

difference in regard to capability and strength of individuals of a given age in different species is stated by Wheeler (:00^b, p. 63). He says that newly hatched queens, as well as worker callows, of Stigmatomma are soon able to run about and to join in the labors of the colony; and they are not so feeble as the callows of more specialized ants. He also says (Wheeler, :07^b, p. 87) that the callows of many ants confine themselves to caring for the larvae and pupae, and do not forage till later.

The difference of brightness occurs in *Camponotus herculeanus pictus*, especially in the thorax, and it has occurred to me to make use of the specimens collected at Randolph, N. H. (see p. 445), in order to see if there is correlation between brightness and various occupations. Of course, as Wasmann (:09^b, p. 39) points out, there is some individual variation in the length of time required for the color to reach its maximum darkness, but it is probable that on the whole the lighter ants are younger, and their strength less developed.

In order to resolve this problem I proceeded as follows: The mounted specimens which had been captured at Randolph, N. H., sharing in particular activities, were first classified according to those activities, and then the ants of each activity were arranged according to color, and compared.

2. *Observations.* — On the whole, the number of light or brightly colored ants was small, but they were of all classes. When the separate activities were observed, the following facts were noticed:

1. In foraging, there were none of the very youngest, though there were a few somewhat lighter than those of the deepest color.

2. There were a few ants engaged in "tending the young" which showed signs of being *very callow*, since they were of such light color that even the legs were very pale. I remember noticing when I collected these that they had not obtained their full strength. There were a good many ants of different sizes in which the thorax had a very bright color, and thus seemed to be young. Most of those which were tending the young under excitement had reached their maximum darkness, though there were a few which were fairly young.

3. Of the few ants which were taken in the act of surrounding a queen, none had obtained their full color, and yet not any were very light colored. This was probably a young brood, the first from that queen, for the queen herself showed signs of being young, and there were only a very few ants in the colony.

4. While most of the ants engaged in building were of full color, there were a very few brightly colored ones.

5. While some of the ants which were being carried were of the maximum depth of color, it is somewhat curious that the majority

were rather light-colored, and some gave evidence of being very young, their color being in general pale, even in the legs. On the other hand, those which were doing the carrying were almost universally dark, and none of them were very bright. Those which were being carried were probably more or less weak.

6. When those which responded to disturbances of the nest were examined, it was found that all had at least nearly reached the maximum depth of color, and most of them had quite reached that stage.

Thus it may be seen that, as has been claimed for other species and for ants in general, the young workers of this species sometimes build, and sometimes are carried about; but they are especially engaged in tending the young (eggs, larvae, or pupae). Occasionally young individuals, though not the youngest, carry other ants, or are found in the field, but only the fully colored ants share in defence.

iv. Conclusions for Camponotus herculeanus pictus.

To summarize the facts concerning *Camponotus herculeanus pictus* when studied in Barth nests or by any of the methods used in the field :

1. No males were seen to share in the duties of workers.

2. The very youngest ants take part especially in tending the eggs, larvae, and pupae, and sometimes in building, and they are apt to be carried by their companions, but they do not go into the field until they are somewhat darker than the very young stages, though they may do so while still retaining some brightness of color. The ants of this species do not, however, enter into the defence of the nest until they are dark.

3. Only a small proportion of the whole number of ants in a colony is engaged at one time in any activity.

4. Though more ants in proportion to the size of the colony are active in large colonies than in small ones, nevertheless this does not seem to make a difference in the kind of individuals engaged in different sorts of work, provided that the colony is of sufficient age to contain ants of all sizes. It must be remembered, however, that in the small colonies in artificial nests rather more large ants, in proportion to the whole number participating, were engaged in the various activities than was the case in out-door nests.

5. All classes may take part in carrying food, but the intermediates are the ones which do this most. Intermediates are also more likely to be found in the field, apparently foraging.

6. While individuals of all classes regurgitate food and receive regurgitated food, it is *probable* that the two smaller classes, especially

the intermediates, are more addicted to regurgitating, and the majors to receiving regurgitated food.

7. In tending the young, the majors are least active, the intermediates more so, and the minors most so. When excited, larger ants enter into this activity somewhat more than they do under normal conditions.

8. In building, all sizes were seen carrying earth, though the two smaller sizes especially excelled in this. In digging, the intermediates were also the more active. The evidence in regard to building is somewhat conflicting, the field notes indicating minors and the Barth nests majors and intermediates as the more active. As the captured ants can, after all, be studied by more exact methods than those in the field, I am inclined to accept as correct the results obtained with the use of nests.

9. Carrying and being carried seem to take place most frequently when the ants are somewhat excited, either by some unnatural disturbance or by the presence of food. These activities are, however, not very common. The process is sometimes one of dragging, but often it is one of actually carrying, and the minors and majors seem often to be transported by other ants, and the intermediates to be carrying them.

10. All three classes took part in licking, but the majors slightly less than the other two classes. The majors seemed never to be licked, and the minors seldom, the intermediates being most often the objects of this activity. The evidence on this activity was, however, slight; nevertheless, it is probable that majors, too, are licked.

11. Ants of all sizes may surround the queen.

12. While all classes will attack an intruder when the nest is disturbed, the majors are the most savage.

13. There is nothing in *C. herculeanus pictus* resembling the process of guarding seen in Colobopsis.

14. There is no hard and fast distinction between classes, either morphologically or physiologically — for in each activity there is a perfectly graded series with no break into classes — but only a *preponderance* of ants of certain sizes in certain activities.

15. The duties in which the small ants, i. e. intermediates and minors, excel may be called the "household duties," and foraging.

16. The majors are relatively inactive in all occupations except fighting, while the other two sizes taken together are very active.

VI. Studies of Pheidole.

A. *Pheidole pilifera.*

i. Experiments with Ants in Aluminum Nests and Other Apparatus.

1. *Methods in General.*

I made use of four colonies of *Pheidole pilifera* from Cambridge, Mass. In order to ascertain whether in these ants there is any correlation between habits on the one hand and size and structure on the other, an attempt was made, as with *Camponotus americanus* (pp. 446–465), to discover what proportion of each class (see pp. 438–440) took part in each of several activities.

In most cases I have endeavored to ascertain (a) the proportion of the whole number of working ants which engage in a given activity, and (b) the relation, if any, between the size of the individuals and the sort of activities which they showed; but in fighting, in carrying, and in partaking of different kinds of food, I have considered only the second of these two matters.

All experiments, unless otherwise stated, were performed in aluminum nests ten inches long, six inches wide, and half an inch deep, kept under the conditions described on pages 440–442, and in all cases both chambers were exposed to daylight and ordinary room temperature during observations. At other times the chamber not containing food was darkened by a pasteboard cover and the nest was placed in the heated chamber.

2. *Feeding Themselves.*

1. *Methods.* — To make sure that all the ants which partook of food were observed, the food, on paraffined paper, was placed in the chamber with the ants, the paper and the food being removed whenever the ants were not under observation. To give the ants an environment as natural as possible, the chamber in which they lived was provided with damp earth. During observations a record was made of the number of ants of each class which partook of food during one hundred and fifty periods of one minute each.

2. *Observations.* — For convenience of comparison, the results of the observations on the various activities of the several species are all placed together in Table VII. Except for fighting, carrying, being carried, and kinds of food, of which mention will be made in appropriate places, this table was compiled as follows. The first column in the table gives the number of the colony, and the first column under each activity shows the number of observations made upon the colony concerning that activity.

TABLE VII.

Species.	No. of the Colony.	Feeding Themselves.							Regurgitating.							Receiving Regurgitated Food.							Licking.						
			Workers.		Sol-diers.		Minors.			Workers.		Sol-diers.		Minors.			Workers.		Sol-diers.		Minors.			Workers.		Sol-diers.		Minors.	
		No. of Observations.	Av. no.	Av. % active.	Av. no.	Av. % active.	Av. no.	Av. % active.	No. of Observations.	Av. no.	Av. % active.	Av. no.	Av. % active.	Av. no.	Av. % active.	No. of Observations.	Av. no.	Av. % active.	Av. no.	Av. % active.	Av. no.	Av. % active.	No. of Observations.	Av. no.	Av. % active.	Av. no.	Av. % active.	Av. no.	Av. % active.
P. pil-ifera.	81	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	86	150	282	0.003	8	0.	274	0.003	100	89	0.01	5	0.	84	0.01	100	89	0.01	5	0.	84	0.01	100	89	0.2	5	0.	84	0.2
	87	..	..	..	..	..	..	..	100	39	0.	7	0.	32	0.	100	39	0.	7	0.	32	0.	100	39	0.7	7	0.	32	0.7
	91	..	..	..	..	..	..	..	100	173	0.01	6	0.	167	0.01	100	173	0.01	6	0.	167	0.01	100	173	0.5	6	0.	167	0.5
P. den-tata.	82	150	42	0.2	21	0.03	21	0.3	150	48	0.03	23	0.	25	0.1	150	48	0.03	23	0.03	25	0.03	150	48	0.2	23	0.	25	0.3
	83	150	6	2.3	3	0.	3	0.4	150	13	0.1	4	0.	9	0.1	150	13	0.1	4	0.	9	0.1	150	13	1.7	4	1.	9	2.9
	84	150	40	0.	4	0.	36	0.	150	59	0.01	5	0.	54	0.01	150	59	0.01	5	0.	54	0.01	150	59	0.4	5	0.	54	0.4
P. vine-landica.	58	150	17	1.1	9	1.8	8	0.3	150	21	0.03	11	0.1	10	0.	150	21	0.03	11	0.	10	0.1	150	21	2.3	11	1.1	10	3.8
		Being Licked.							Tending Young.							Building.							Surrounding Queen.						
P. pil-ifera.	81	..	..	..	..	..	..	..	..	..	..	..	..	..	..	150	12	0.8	4	1.4	8	0.6	..	..	..	..	..	..	..
	86	100	89	0.2	5	0.	84	0.2	..	..	..	..	..	..	..	100	112	2.	5	1.	107	2.	..	..	..	..	..	..	..
	87	100	39	0.6	7	0.4	32	0.6	..	..	..	..	..	..	..	100	38	0.4	6	0.	32	0.4	..	..	..	..	..	..	..
	91	100	173	0.5	6	1.	167	0.5	100	193	2.6	6	0.	187	2.6	100	157	0.2	6	0.	151	0.2	..	..	..	..	..	..	..

P. dentata.	82	150	48	0.2	23	0.1	25	0.2	150	42	0.3	21	0.2	21	0.6	150	42	6.9	21	3.2	21	11.1	..	..	..	..	..	..	..
	83	150	13	2.2	4	3.3	9	1.7	150	16	2.	5	0.	11	2.5	150	6	3.2	3	0.7	3	5.7	..	..	..	..	..	..	..
	84	150	59	0.3	5	0.1	54	0.3	150	70	3.1	5	0.9	65	3.9	150	43	0.8	4	1.1	38	0.9	..	..	..	..	..	..	..
P. vinelandica.	58	150	21	2.2	11	2.6	10	1.6	150	141	2.4	28	0.	113	3.1	150	113	6.3	26	1.2	87	7.2	41	74	12.4	20	11.9	54	13.4

		Guarding.							Fighting.					Carrying and being carried.					Kinds of Food.									
		No. of Observations.	Workers.		Soldiers.		Minors.		No. of Observations.	Soldiers.		Minors.		No. of Observations.	Soldiers.		Minors.		No. of Ants Feeding.	Meal-worm.		Honey.		Grass-seed.		Apple.	
			Av. no.	Av. % active.	Av. no.	Av. % active.	Av. no.	Av. % active.		Av. no.	Av. % active.	Av. no.	Av. % active.		Av. no.	Av. % active.	Av. no.	Av. % active.		% Sold.	% Min.	% Sold.	% Min.	% Sold.	% Min.	% Sold.	% Min.
P. pilifera.	81	150	4	0.	2	0.	2	0.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	86	100	108	0.2	5	0.	103	0.2	50	8	27.9	8	25.6	3	6	0.	163	7.3	1	100.	0.	0.	0.	0.	0.	0.	0.
	87	100	34	0.1	6	0.	28	0.1	50	11	18.7	11	6.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	91	100	154	0.03	6	0.2	148	0.03	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
P. dentata.	82	150	42	1.2	21	0.9	21	1.7	..	..	..	..	..	..	..	..	..	..	12	0.	16.7	8.3	50.	0.	0.	0.	25.
	83	150	6	2.2	3	1.3	3	2.9	..	..	..	..	..	1	4	0.	9	11.	3	0.	33.3	0.	33.3	0.	0.	0.	33.3
	84	150	40	0.	4	0.	36	0.	50	4	24.5	4	6.	10	5	0.	49	3.	0	0.	0.	0.	0.	0.	0.	0.	0.
P. vinelandica.	58	150	47	0.7	18	1.4	29	0.3	..	..	..	..	..	..	..	..	..	..	15	66.7	0.	20.	13.3	0.	0.	..	..

The second column under each activity gives the average number of workers in the colony, the fourth and sixth the average numbers of the two classes of workers (soldiers and minors, respectively) in the nest during the observations on that activity. It was necessary to take the *average* number rather than the *total* number, because of the death of some individuals between series of observations when the whole of an experiment on a colony could not be carried out at one time. In many cases this was equal to the total number of individuals at the beginning of the experiment, no deaths having occurred. The third, fifth and seventh columns under each activity give the average per cent of the workers as a whole and of the respective classes (soldiers and minors) which took part in each activity. These were found by dividing the sum of the per cents of those which were active at each observation by the total number of observations, usually 150. Dots signify that a particular experiment was not made upon the colony opposite which the dots appear, as, for instance, opposite colony 81, "feeding," "regurgitating," etc. This was usually due to the death of the whole colony before the experiment on that form of activity could be carried out, but in the case of "surrounding the queen" the absence of records is due to the fact that most of the colonies had no queen. Colonies 81, 86, 87, and 91 were *Pheidole pilifera;* 82, 83, and 84 were *P. dentata;* while colony 58 was *P. vinelandica.*

Of *Pheidole pilifera*, only one colony (86) was tested in the matter of feeding. Of all the workers, including both soldiers and minors, the per cent engaged in feeding was small (0.003 per cent). In this case, the soldiers did not take part at all.

3. *Regurgitating and Receiving Regurgitated Food.*

1. *Methods.* — As these two sets of activities are necessarily reciprocal, they were noted at the same time. At two-minute intervals the number of ants of each class engaged in regurgitating food was recorded, and likewise the number of each class which were receiving regurgitated food. As the ants were inclined when opportunity offered to hide in the earth, a wet sponge, to provide both drinking water for them and dampness for the atmosphere, was substituted for earth. To prevent the ants from hiding in this sponge it was wrapped in cheese cloth, the edges of which were securely sewed together so as to leave no openings. When this was done great care had to be taken to prevent the sponge from drying. This sponge was placed in one chamber and food in the other.

2. *Observations.* — Three colonies of *Pheidole pilifera* were observed in these experiments. Here, again, there were very few ants (0.01 per

cent) actively or passively engaged, and in one of the three colonies (87) there was no such activity during my observations. In each of the other two colonies the percentage engaged in this process was about equal, but as there was considerable difference in the whole number (89 and 173) of ants in these colonies, it follows that the number engaged is not closely correlated with the number of ants in the colony.

In this species I saw no soldiers either regurgitating or receiving regurgitated food. In one nest, as before stated, this activity was not seen at all; in the others, minors fed minors, 0.01 per cent giving and 0.01 per cent receiving food in each colony. In this species, then, so far as my observations go, regurgitating is limited to the minors.

4. *Licking and Being Licked.*

1. *Methods.* — These two sets of activities, being also reciprocal, were observed at the same time. In one chamber was a wet sponge covered with cheese cloth; in the other, food. Observations were made once every two minutes, and the number of ants of each class, both those licking other ants, and those being licked, was recorded separately.

2. *Observations.* — One hundred observations were made on each of three colonies. Here, too, only a few ants licked or were licked (0.2 per cent, 0.7 per cent, 0.5 per cent; and 0.2 per cent, 0.6 per cent, 0.5 per cent), and the per cents of ants so engaged in the different colonies of the species do not agree closely. In this species of Pheidole the proportion of ants engaged seems to be independent of the total number of ants in the colony.

In all cases in this species the minors were more active than the soldiers, as the latter did not lick other ants at all. In the matter of being licked, two colonies gave more minors (0.2 per cent $>$ 0 per cent; 0.6 per cent $>$ 0.4 per cent), and one, more soldiers (0.5 per cent $<$ 1 per cent).

5. *Tending the Young.*

1. *Methods.* — In this experiment it was not practicable to have earth on the floor of the nest, as the ants were inclined to make use of the earth in which to hide their young; therefore a wet sponge covered with cheese cloth was put into one of the chambers, while the food was placed in the other. At intervals of one minute a count was made of the number of ants of each class holding young in their mouths, or otherwise seeming to care for them. As an individual in possession of young frequently held them for a long time, the young, after each ob-

servation, were taken from any ants carrying them, and placed on the floor of the nest, so as to give all ants as nearly as possible an equal chance to pick them up.

2. *Observations.* — One hundred observations were made on a single colony of *P. pilifera.* The other colonies contained no young. In this colony only a few workers (2.6 per cent) were engaged in this activity, no soldiers sharing in it.

6. *Building.*

1. *Methods.* — In order to watch the ants while building, one chamber was provided with damp earth. This was placed on the floor of the chamber, and was of such depth that the ants could not wholly secrete themselves in it. Food was placed in the other chamber. As an aid in counting the ants, the pane of glass which covered the chamber containing earth was ruled into half-inch squares. Observations were made at five-minute intervals in the case of one colony (81); in all other cases the interval was two minutes. At each observation a count was made of all ants of each class which were either digging or carrying earth.

2. *Observations.* — One hundred and fifty observations were made on colony 81, and on the others (86, 87, 91) one hundred each.

Although the per cent of active ants here was somewhat greater than in the activities previously considered, still it was small (0.8, 2, 0.4, 0.2). It was not correlated with the whole number of ants in the colony.

In two colonies (87 and 91) the soldiers did not build at all, and in one of the others (86) the minors were the more active (2 per cent > 1 per cent), in the remaining colony (81) the soldiers were the more active (0.6 per cent < 1.4 per cent). Considering all the colonies together, the greater activity was decidedly on the part of the minors.

7. *Surrounding the Queen.*

As there were no queens in any of the colonies of *Pheidole pilifera*, I was obliged to omit observations in regard to this subject on this species.

8. *Guarding.*

1. *Methods.* — For the purpose of observing which individuals served as guards to protect or warn the colony in time of danger, the ants were allowed to build a nest of earth in one chamber; food was placed in the other. In order to stimulate the ants and to discover whether any individuals were stationed as guards at the entrances of the earth

nest, and if so, to which class or classes they belonged, the entrances to the nest were probed with a bristle either once every five minutes (colony 81) or once every minute (colonies 86, 87, 91). The number of ants of each class emerging from these entrances at each observation was recorded. Often the first individual to come from the entrance attacked the bristle with widely opened jaws, in some instances even clinging to the bristle. Sometimes, however, it rushed out excitedly, with open jaws, and then hurried back into the hole, whence it often emerged again, sometimes followed almost immediately by one or more other ants. In such cases the class to which these accompanying ants belonged was also recorded, though they were not considered as belonging among the original guards.

2. *Observations.* — Four colonies of *Pheidole pilifera* were experimented on by making one hundred and fifty observations on colony 81, and one hundred observations on each of colonies 86, 87, and 91.

Only a very small per cent (0; 0.2; 0.1; 0.3 respectively) were engaged in this activity, one colony giving no response; moreover, the number was not correlated with the whole number of ants in the colony.

In two of the responsive colonies (86 and 87) of this species, the soldiers were not represented; in the other they were slightly more active than the minors ($0.2 > 0.03$); but we may say of this species that on the whole the minors were the more active.

9. *Fighting.*

1. *Methods.* — In this activity it was impossible to deal with per cents of the colony as a whole, because when an enemy was introduced, all the ants of the colony rushed about in such a lively and excited manner that it was out of the question to count even those which attacked it. Accordingly the soldiers of the colony were placed in a Stender dish, 5.5 cm. in diameter, and an equal number of minors were placed in another Stender dish of the same size. If a minor was killed, another was put in its place, but if a soldier was killed, the number of minors was reduced by removing one of the minors, so that the number of ants in the two dishes was constantly equal. The observations consisted in counting for one-minute periods the number of ants clinging to an enemy which was placed for that length of time alternately with the soldiers and with the minors. The enemy introduced was an ant from a colony of *Camponotus americanus.*

2. *Observations.* — Fifty observations were made on each of two colonies of *Pheidole pilifera* (colonies 86 and 87). Under "Fighting," and "Carrying and Being Carried," in Table VII the first column gives

the number of observations, the second and fourth the average number of soldiers and of minors respectively used in the experiment, and the third and fifth columns the average per cents of soldiers and of minors respectively which took part in this activity.

It will be noticed that in fighting, the per cents of ants attacking an enemy are fairly large (27.9, 18.7 ; 25.6, 6.3) and that the soldiers were much more active than the minors.

10. *Carrying and Being Carried.*

1. *Methods.* — These activities occurred so rarely that I have not experimented in regard to them. However, when I have seen one ant carrying another, I have recorded the fact, as well as the class to which each belonged, and the number of each class present in the colony at the time of the observation, so that I might judge of the proportions, which would be in some degree comparable with those in the other activities. Though these observations were few, perhaps too few to make it safe to draw conclusions from them when they stand by themselves, nevertheless, in connection with other observations on the same activities, they may have some value.

2. *Observations.* — Carrying was observed to take place in only one colony (86) of *P. pilifera.* In this colony no soldiers were active in either carrying or being carried. The per cent of minors (7.3 per cent) engaged in carrying and being carried was therefore the same, and one table answers for both.

11. *Partaking of Different Kinds of Food.*

1. *Methods.* — According to the accounts of Reichenbach ('96, p. xcv) and Wheeler (: 02, p. 770), it seems probable that different classes of ants have different tastes in regard to various *kinds* of food and different ways of treating it. Accordingly, while making my other observations on feeding, I have tried to discover whether one class interests itself in certain kinds of food and the other class in other kinds. To this end I recorded the class to which each ant seen at the food belonged, and also the kind of food of which it was partaking.

2. *Observations.* — One colony (86) of *P. pilifera* was observed, and in this colony only one ant (a soldier) ate, its food being a mealworm. During these observations no ant ate grass-seed. That this species does eat grain, and even grass-seed, I feel sure from Wheeler's (: 05[d], p. 380) observations and from my own observations in the field; moreover Wheeler states that in the grain-storing species of Pheidole, the soldiers act as seed crushers for the community.

12. *Relation of Classes to Various Activities.*

From the foregoing account it is evident that, at least under the conditions employed, both classes of *Pheidole pilifera* share in most of the activities which were examined. In treatment of seed, no activity was shown by either class. The soldiers of this species took no part in either feeding, tending the young, regurgitating, receiving regurgitated food, licking, carrying or being carried; but they were more active than the minors in fighting. In being licked, the two classes shared nearly equally, but in all other activities the minors excelled (feeding, regurgitating, licking, tending the young, building, and carrying), occupations which may be called "household duties." Carrying, in which the minors alone engaged, may be correlated with the size of the head, for the body of a minor would be better balanced when performing this duty than would that of a soldier. Guarding, though shared apparently to a greater extent by the minors, seems to be more or less accidental, and does not here consist — as in Colobopsis and a species of Pheidole recorded by Reichenbach — of blocking the entrances of the nests with the head. If it did, we should expect to find always the same sort of worker at the same opening, which is not the case in any of the species of Pheidole which I have studied. The act of guarding seems here to be rather the result of the fact that, as ants pass in and out, or are otherwise near an opening, they rush out when disturbed. Now, the soldiers are not apt to leave the nest, and hence are probably not as often near the openings, which would account for the greater number of minors found guarding.

But if the minors are pre-eminently occupied with household duties, the soldiers seem to be concerned with occupations requiring strength of jaw, such as fighting, and though the minors help them in this, there is much difference between the two classes in regard to this activity. Moreover, when in the presence of the enemy, the soldiers ran about snapping their jaws in a much more ferocious way than did the minors, and they never ran away, whereas the minors frequently did. We may, then, say that in this species the minors are, in general, more concerned with "household duties," and the majors with fighting, and, as Wheeler has shown, with crushing seed.

II. Studies of Pheidole pilifera in Barth Nests.

1. *Methods.* — The methods here employed were exactly like those described for *Camponotus pictus* (pp. 443 et seq., 465), except for the difference in size of the nests. These nests were 5 inches in diameter,

$4\frac{3}{4}$ inches high, and had $\frac{1}{4}$ inch space between the two jars. Two colonies were under observation.

2. *Observations.* — There were neither queens nor young of *Pheidole pilifera* in the nests, and hence evidence on the activities of surrounding the queen and tending the young is necessarily wanting. Only a small part of the colony took part at any one time in any of the activities observed.

Though I several times tried the same experiment with the meal-worm which was tried in the field (p. 486), I never got a response. This experiment consisted in placing a meal-worm near the nest, and noticing whether either class broke it to pieces.

Unfortunately the ants all died before I was able to try any experiments on fighting. I had purposely left this experiment till the last, because of its destructive outcome. However, if responding to a disturbance of the nest caused by knocking on the glass or tampering with the earth at the top of the nest be any indication, it may be said that both classes respond pretty generally every time; but the soldiers seem to be much more excited than the minors by such stimuli.

I did not see any scavengers in these nests.

In regard to foraging, the minors were seen in the well and on top of the earth much oftener than the soldiers; the latter kept almost wholly underground.

No soldier was ever seen carrying in food or preparing seed, but a few minors were noticed doing both of these things, especially the carrying of food. Once, however, when a minor brought in a seed and placed it near a soldier, the latter became excited, waving its antennae in the air. Presently it left the chamber, but returned almost immediately, and for a short time remained near the seed perfectly quiet. Soon it left again, and did not return while I watched the nest; where it went I was unable to see. It did not at any time touch the seed, and the cause of its excitement may have been something wholly different. Once I saw a soldier carry a seed from one part of the nest to another; and on another occasion four small ants each tried unsuccessfully to drag a soldier toward a pile of seed. When the small ants broke up seed, they sometimes pulled at different parts of the same husk, and sometimes each attacked a seed alone, pulling off pieces of the husk with its jaws. Chaff was commonly found in the deeper parts of the nest and under the well. Though "breakfast foods" of various kinds ("Quaker" oats, hominy, rice, corn meal) were placed on the surface of the nests, I never saw the ants split these. They were carried in, however, especially the Quaker oats, but the ants seemed to much prefer grass-seed.

On only a few occasions did I see minors feeding themselves, and soldiers never; nor did I see the latter receive any regurgitated food.

The small ants were much more likely to lick other ants than were the soldiers, of which I saw only one engaged in this performance. The minors were just as much inclined to lick one class as the other.

Though I did not see many ants engaged in building, there was a division of this kind of labor between the two classes. The carrying of earth was all done by the minors, whereas all the digging observed was the work of soldiers (four individuals, not all from the same colony). The digging consisted of using the front feet, much as a dog does in digging a hole in the ground, and also in breaking off pieces of earth with the jaws. I have also seen soldiers, by squeezing their way through narrow passages in the galleries, loosen earth, which the minors then carried away.

Only minors have been seen dragging other ants, and only soldiers were being dragged. Had those which were being dragged been small enough, they probably would have been carried, for this activity seems to correspond to that which is properly called "carrying" in cases where the ants being transported are small; such, for example, as were observed in this species, both in aluminum nests and in the field, and likewise in Camponotus (p. 468).

To sum up the facts concerning the relative participation of the two classes in the various activities as far as observed in Barth nests, it may be stated that all the digging was done by soldiers, and that they were more excited in responding to disturbances of the nest, but that in all other functions they were less active, not sharing at all in some of them. There was no evidence of guarding.

iii. Out-door Work on Pheidole pilifera.

1. *Methods.*

Essentially the same methods were used in studying *Pheidole pilifera* as in that of *Camponotus pictus*, except that, owing to the distinctness of classes, it was possible to make and record final observations as to class without the necessity of killing and preserving for subsequent study so large a number of ants observed in the different activities. There are occasionally individuals intermediate in form between the extreme classes, but they are so rare as to cause no danger of confusion. I have had so little chance to observe them that I am not prepared to say just what their functions are. Frequently records were made of the number of ants of each class in a colony seen engaged in a given occupation during a certain period, usually of

five minutes' duration. Sometimes ants of this species were captured and preserved in alcohol and then mounted in series, as described above for Camponotus (p. 469). Eighteen colonies were studied.

2. *Observations.*

1. *Field notes.* — In these studies, as in those on *Camponotus pictus*, certain activities were not recorded. This was due to the fact that, for the most part, these activities are carried on below ground, and hence are not to be seen without disturbing the nest.

In regard to the other activities, it appeared that here as in *Camponotus pictus* when studied in the field, the proportion of ants engaged in any activity at one time was very small in relation to the total number of ants belonging to the colony. On the whole, the minors are much more alert in all activities, it being only rarely that the soldiers take any part at all. Thus, carrying food, tending the young, carrying other ants, fighting and scavengering are functions in which only the minors take part; while in other duties (foraging, cutting up meal-worms, carrying earth, and being carried), though both classes participate, the minors exhibit the greater activity. I have never seen the soldiers eating in the field. There is, moreover, no function which belongs exclusively to the soldiers. The question is whether there is any function to which this class is exclusively adapted. Wheeler (:02, p. 770) says that in Pheidole, the soldiers of the grain-storing species crush seed, breaking up the hard shells, while those of the carnivorous species cut up the hard chitinous joints of insects. He states that, in some species, the soldiers deserve their name, while in others they are cowardly. I have never seen *Pheidole pilifera* in the field tearing seeds apart or crushing them. As to cutting to pieces large insects, I have frequently seen the soldiers pass by large insects which they found in the field, or the meal-worms which I placed near the entrances of the nests, whereas the same food was frequently carried in by the minors, either in separate bits or as a whole, by the combined action of a number of ants. Only once have I seen a soldier engaged in cutting up an insect. On this occasion I placed a meal-worm, which was dry and had been partly eaten by its comrades, near the entrance of the nest where many minors were going and coming. Almost immediately two minors began to feed on it, and others soon joined them. After five minutes, when one had eaten, it entered the nest, and almost immediately a number of other minors emerged and began to eat the meal-worm. Then they began to break off bits of the insect and to carry it into the nest. All the ants which emerged from the entrance now went to the meal-worm. After fifteen minutes the

first soldier made its appearance, and with its huge jaws began to cut the meal-worm, always returning to the nest after every three or four cuts had been made. After a time the ants tried to carry the whole carcass into the nest, but found it too large, so they only succeeded in moving it to the entrance. I do not feel sure whether or not the soldier carried any pieces into the nest, but the minors certainly did, and they also broke off little bits. If the soldier carried nothing back into the nest, I am at a loss to explain why it kept returning there. This is the only time I have seen such a performance. It would seem that while the soldiers of this species sometimes cut up insects in the field, it is not very common for them to do so; but perhaps this sort of work is carried on to a greater extent within the nest.

In regard to fighting, I tried a number of times throwing down a colony of Lasius (sp ?) upon a Pheidole nest. Sometimes no fight followed, the ants of the two species not happening to meet each other; but when a struggle did ensue, the soldiers were much more sluggish than the minors, which attacked Lasius vigorously. Even when the soldiers came in contact with the enemy, they did not succeed in grasping them, though they snapped at them. Possibly the Lasius workers were too quick for them, or the jaws of the Pheidole soldiers are not adapted for grasping the legs of Lasius. However, I have already (pp. 481–482) given evidence to show that the soldiers of *Pheidole pilifera* do fight. Forel ('**74**, p. 246) describes the different manner in which ants fight with enemies larger or smaller than themselves. When the enemy is larger, the small ants try to grasp its antennae or its legs, which is just what happened when Pheidole was fighting with Camponotus. But Lasius, though slightly larger than Pheidole, was more nearly of the size of Pheidole, and the small workers were therefore better able to cope with Lasius than with Camponotus.

From the field-notes on *Pheidole pilifera*, then, it appears that the minors are, on the whole, much more active than the soldiers. The soldiers in the field appeared very sluggish, moved more slowly than the minors, and were rarely occupied.

2. *Captured Ants.* — The studies on captured specimens of *Pheidole pilifera* yielded the following results: Out of a total number of 288 ants collected in the field, around the natural nests, only four were soldiers. Of these 288 ants, 92 minors and only one soldier carried food. There were thirty-seven minors and no soldiers captured building, i. e. carrying earth out of the nests; five minors and no soldiers tending the young under conditions causing excitement; one soldier being carried, and two minors carrying. From this it is evident that,

at most, the soldiers take little part in these occupations. Of the minors which were taken empty-mouthed in the field, one was hardly half the normal size, and was very light in color.

iv. Conclusions from all Studies on Pheidole pilifera.

1. Only a small portion of the whole colony is engaged in any of the activities of the colony at any one time, whether observed in the laboratory or in the field, though in the field the proportion is larger than in the laboratory.

2. The proportion of ants engaging in any particular activity is probably not closely correlated with the number of ants in the colony, though in very large colonies more ants take part than in very small ones.

3. The size of the colony does not seem to make much difference as to kind of ants engaging in the various activities, so long as both classes are present, and there is not great difference in the sizes of the colonies. Moreover, the classes behave in essentially the same manner in this respect whether the colonies are studied in the laboratory or in the field. There are, however, more ants of each kind active in the out-door nests than in the artificial ones, and on the whole, a greater proportion of soldiers are active in the laboratory than in the field.

4. The minors were much more active than the soldiers in obtaining food for themselves.

5. No soldiers were seen regurgitating or receiving regurgitated food, but minors regurgitated to minors.

6. No individuals were seen to eat grass-seed, but a soldier ate meal-worm when caged in an aluminum nest.

7. Minors alone took part in carrying in food, with the exception of one soldier which was captured, though soldiers were occasionally seen in the field, and once a soldier was observed carrying a seed from one part of a Barth nest to another.

8. In scavengering, only minors took part.

9. No soldiers broke or crushed grass-seed, though such seed is found in the nests, and minors carry it home. Minors, however, have been seen breaking seed.

10. Both soldiers and minors were seen cutting up a meal-worm.

11. The minors were active in licking, but I saw only one soldier taking part in this occupation, this one being in a Barth nest. Both classes were licked, but the minors somewhat more frequently than the soldiers.

12. No soldiers showed any evidence of taking part in tending the

young, even in the out-door colonies when excited, but the minors were fairly active.

13. The greater activity in building was decidedly on the part of the minors, though both classes carried earth and both dug. Probably the soldiers, with their large jaws, are better fitted to do this work than they are to share in some other functions, such as tending the young, for example, and hence their relatively increased activity in this duty.

14. There was no guarding of the kind observed in Colobopsis by Wheeler and by Forel. However, when the entrances of the nests were disturbed, both classes were inclined to rush out, though the minors were somewhat the more active.

15. When confined in Stender dishes it was found: First, that the proportion of ants engaged in fighting is unusually large for both soldiers and minors. This is probably due in part to the difference of methods from those employed for the other activities, the ants being here confined in so small a space as to have a very large chance of stimulation; and in part to the nature of the activity, which is of such a character that we should expect a large proportion of individuals to share in it. Secondly, the soldiers were much more active in fighting than were the minors, and they were more successful in grasping the legs and antennae of Camponotus, while the minors seized the body hairs of their enemies. On the other hand, in the field, the minors seemed more successful in fighting with Lasius. The soldiers were much more active in responding to disturbances caused by knocking on the nest.

16. In aluminum nests no soldiers were active in carrying or being carried. In Barth nests, soldiers were dragged more commonly than minors, but did not drag or carry other ants.

17. The minors show greater activity in foraging and in all "household duties."

18. The minors are much more lively in those activities in which they share than are the soldiers.

19. There is no hard and fast line between the duties undertaken by separate classes, and in most duties all individuals are capable of sharing. There is, nevertheless, in each activity a *preponderance* of ants of a certain class taking part.

B. Studies on Other Species of Pheidole.

1. *Methods.* — Three colonies of *Pheidole dentata*, from Austin, Texas, and one of *Pheidole vinelandica*, from Highlands, New Jersey, were studied in exactly the same way as *Pheidole pilifera* in aluminum

nests and other apparatus, except for slight differences in the number of observations or in the length of time of the observations. I had no opportunity for studying these ants by the other methods used on *P. pilifera*.

2. *Observations.* — Since the conclusions for these two species in the main closely resembled those for *P. pilifera*, I have considered them merely as a control, and I shall give only the points in which they differ from *P. pilifera*. The numerical values are given in Table VII.

I. *Pheidole dentata.*

1. In *Pheidole dentata*, though the minors were more active in regurgitating, as also in receiving regurgitated food, soldiers appeared to take some part in receiving regurgitated food.
2. Occasionally soldiers were seen carrying larvae.
3. No soldiers were observed carrying other ants, and only minors were carried.
4. Only minors ate meal-worms. Both classes ate honey.
5. No soldiers and no minors were seen to crush, break, or eat grass-seed. This is what we should expect, since *Pheidole dentata* is a purely carnivorous species.

II. *Pheidole vinelandica.*

1. Surrounding the Queen. (a.) *Methods.* — This was the only species in which I had a colony containing a queen. The ants of this genus have, like other ants, a tendency to gather in groups around the queen. The number of ants of each class sharing in this grouping was noted once every five minutes. To keep the ants from secreting themselves under the sponge, thus making observation difficult, the sponge was removed. There was food in one chamber.

(b.) *Observations.* — Only 41 observations were made on the colony of *P. vinelandica*, because the queen died before further observations were possible. The proportion of workers surrounding the queen was somewhat higher (12.4 per cent) than in any of the other activities.

In this case both classes shared in the activity, but the minors were more active than the soldiers (13.4 per cent $>$ 11.9 per cent).

2. Though the soldiers, when confined in artificial nests, *seemed* more active in feeding, the minors of this species appeared to me to be much more numerous around the natural nest in the field, even in proportion to their numbers in the colony. If more than one colony had been accessible at the time of the experiments in the artificial nest, the results with this species might have resembled those with the other species more than these records show. There are two possible expla-

nations for the apparent greater activity of the soldiers of this species in feeding: First, the amount of difference between the two classes may not be real, both being about equally concerned in this activity. Secondly, the greater activity of the minors in the field may be due to the fact that they collect more food than they need for themselves, and later regurgitate it from their crops to other individuals. In the case of colony 58 they may have taken only enough for themselves, so that they were here less active than usual, and in consequence, the soldiers appeared relatively more active. In view of the facts that the minors usually regurgitate and soldiers receive, that soldiers at best give out food only very seldom, and that soldiers of *Pheidole pilifera*, and probably also of this species, appear only rarely in the field, I am inclined toward the second explanation.

3. The soldiers were more licked than were the minors.

4. Though, as in *P. pilifera*, the minors were most concerned in tending the young, on one occasion a soldier was seen with young in its mouth.

5. In surrounding the queen, both classes took part, the minors being somewhat more active than the soldiers. This was the only colony of Pheidole in which this activity was tested.

6. Though the nature of guarding resembled that found in *P. pilifera*, the soldiers in *P. vinelandica* seemed much more active than the minors.

7. Though carrying and being carried were looked for, no cases were observed.

8. No individuals of either class crushed or broke up grass-seed.

VII. Discussion.

Having given in the historical part of this paper some account of the work of other writers on division of labor among ants, and having recorded my own observations on several species, we may now state such conclusions concerning the division of labor as seem warranted by the facts already established.

1. It will be remembered that Forel ('**95**, p. 146) and Escherich (:**06**, p. 45) state for ants in general that polymorphism goes hand in hand with division of labor. Many examples of this are cited in the historical part (II) of this paper.

Of the species which I have studied, *Camponotus americanus* and *C. herculeanus pictus* are examples of a graded series of workers extending from the smallest to the largest with no break in the line, and in many characteristics the queen closely resembles the largest worker.

Pheidole pilifera, *P. vinelandica* and *P. dentata*, on the contrary, belong to the group described by Emery ('94, p. 55) as having two classes of workers, the extremes not being connected by intermediates.

The large size of the larger workers of Camponotus, especially the great size of the head and its disproportionate width, which are correlated with greater strength of jaw, adapts them particularly for combatting enemies and for work requiring great strength. The small workers, owing to their size, are better adapted to pursuits which require agility. However, their jaws and the general proportions of their bodies probably fit them better for carrying loads, such as larvae, pupae, earth, wood, food, etc. In the workers, the position of the eyes, the depth of the head, and the shape of its posterior margin are probably caused by the greater development of the clypeus and the mandibles. But in all these structures there is a gradual transition in size from one end of the series to the other.

In *Pheidole pilifera*, however, the case is different. Though the same parts of the head that are variable in *C. herculeanus pictus* are also subject to variation in this species, there is not a graded series; there are only three well-marked conditions, a queen, a large worker and a small worker. The small worker, especially because of its weak mandibles, which are toothed, seems adapted to only the lighter work of the colony, while the soldier, with its peculiar mandibles, is better adapted for heavy work or fighting. The queen resembles in some respects the small worker, in others the large one. The characters of the queen which least resemble those of the small worker, become especially prominent in the soldier, which has, in addition, certain modifications of structure depending on the enormously developed mandibles. It seems that we have a case in harmony with the view of Emery ('94) and of Wheeler (:07[b]; :10), that the large workers resembling the queen were the primitive form, that the small workers were developed later as the result of gradual diminution in size, and that the intermediate forms then disappeared, leaving the extremes as two separate classes, and that in addition the large workers became enormously developed along certain lines.

2. These forms, Camponotus and Pheidole, have been compared with each other for the purpose of discovering, if possible, whether there is any difference in the distribution of functions in the classes of the two genera. With this end in view a larger number of activities has been studied in each group than has hitherto been examined in any one species. Though it was found that artificial conditions made some difference in the proportion of active ants, there does not seem to be

much difference in respect to the *sort* of individuals which participate *most* in each occupation, for the results in this respect seem to agree fairly well for each species, whether studied in the laboratory or in the field. This statement must, of course, be understood as applying to such colonies only as have attained sufficient size to contain individuals of all classes. Furthermore, it was found in both Camponotus and Pheidole that in the small colonies which were used in the laboratory the larger ants did more work than they do in the field. This is probably due to a reversion on their part to queen instincts (p. 464). It was found that in both genera the investigated activities of the classes generally overlap; that is, the activities are not limited exclusively to one class, but probably all individuals share more or less in all activities. In general, however, there appears to be in certain activities a preponderance of large ants, and in certain others of small ones. For example, in *Camponotus americanus* the small individuals seem to be engaged especially in tending the young, the minors and intermediates together in building, the intermediates in foraging, and the majors in fighting. In *C. pictus* the minors are especially engaged in tending the young; the intermediates in carrying food, in foraging, and in carrying other ants; and the minors and intermediates together in regurgitating (probably), in building, and in licking other ants. In *Pheidole pilifera* there is no intermediate class, but all these duties are performed by the small workers. Moreover, when, as occasionally happens, intermediates are found, they more often approximate the size of the small than the large workers, and even the shape of the head is not wholly like that of the soldiers. In Camponotus there is a slightly greater break between the functions of the majors and those of other ants than there is anywhere else in the worker series, though there is less difference in structure between the extremes than there is in Pheidole. Nor is there as much difference in behavior between the majors and minors of Camponotus as between those of Pheidole. It therefore seems as if the two classes of smaller individuals, the minors and intermediates, taken together, share in the work which in Pheidole is accomplished by the small ants. Again, the soldiers of Pheidole and the majors of Camponotus both seem to take a more active part in fighting than do the other workers of either genus. In some species of Pheidole, however, according to Wheeler (:02, p. 770), the soldiers are cowardly and not inclined to fight. Furthermore it has been established by Wheeler (l. c.) that in Pheidole the soldiers of some species prepare insect food, or grain, so that it may be carried home or eaten. I, also, have seen some evidence of this. The small workers, as I have shown, also undoubtedly share in this. It is seldom that

the soldiers of Pheidole are seen in the field, and when they are, they are usually idle.

3. It was found in *Camponotus americanus* and I have no reason to doubt it is likewise true of the other species of this genus and of the species of Pheidole which I studied, and, indeed, for ants in general) that a few individuals were much more active than the others, not only in foraging, as was proved by Lubbock ('**82**) for certain species, but also in building and in tending the young; and these more active ants were not all of the same size. Moreover, some of them were about equally concerned in more than one activity. This is probably due to such individual psychical differences as those to which Escherich (:**06**, p. 45) refers, and is in agreement with the statement of Fielde (:**03**[d], p. 621) that "a few individuals among ants do most of the work undertaken."

4. In both Camponotus and Pheidole, there were many more ants in the colony than were active at any one time. This was true not only in artificial nests, but also, though to a less extent, in the field. Lubbock ('**82**) found this limitation of activity to be very striking in his artificial nests of *Formica fusca* and Polyergus containing "*the usual slaves*," though the numbers of ants in his colonies were much smaller than those in mine. The artificial conditions, which were unavoidable in such nests as either of us have used, must evidently be responsible for the very small number of ants which were active under these circumstances, as compared with the conditions out of doors. But the proportion of active ants in my colonies was much larger than in his. Although it was found that the proportion of individuals which were active in natural nests was much greater than in the artificial nests of the laboratory, nevertheless, when compared with the size of the whole colony, the number is surprisingly small even in the natural nests. In Camponotus it is, to judge from my own observations, somewhat smaller than in Pheidole.

It was also found that the number of individuals which are active in a colony is not closely correlated with the whole number in the colony, for often more ants are found to be active in a very small colony than in one slightly larger. It is certain, however, that if a very large and a very small colony are compared, the large colony will be found to have many more individuals at work than the small one.

5. In regard to the kind of work done by individuals at different ages, it may be said that my studies on *C. herculeanus pictus* confirm the statements of Forel ('**74**, p. 262), Peréz (:**00**, p. 769), Wheeler (:**07**[b], p. 87), and others, that ants when they emerge from the pupal state attend especially to nursing and somewhat to other duties within the

nest, but that they do not go into the field until they have nearly reached their darkest color, and that they do not fight until they have completely attained that condition. It has been stated by Fielde (:03[c], p. 321) that if ants from different colonies, even of different species, are placed together within twelve hours after hatching, and if they touch all the other ants with their antennae during the three days following, they will live together peaceably. She further states (Fielde, :02, p. 541) that before an ant is five days old it has all its reflexes determined. The fact that ants when very young do not fight at all would account for the possibility of forming mixed colonies, as just described. Probably by the time their fighting instincts are developed, they have become so used to one another that they have no inclination to fight. The same would probably also be true of ants emerging from the pupal state under similar conditions in out-door colonies.

6. Some attention was paid to the kinds of activity in which the queens of colonies of various sizes engaged, in order that queens and workers might be compared. While the queens of those species of Camponotus which were studied are capable of bringing up colonies and of doing all the work necessary for this, it was found that in large colonies they commonly serve merely as egg-layers, except possibly in time of danger; but in small colonies, even in those which are of sufficient age to contain workers of all sizes, their instincts occasionally cause them to revert to other occupations, and to share in such activities as building and tending the young. Indeed, Wheeler (:04[a], p. 156) found a queen of Colobopsis guarding the entrances of the nest, and says (:03[c], p. 45), "So far as I was able to observe, both the virgin and the deälated females of Leptothorax behaved in all respects like the workers," and, "it should also be noted that in artificial nests consisting exclusively of female Myrmicas and Leptothorax colonies, the former behaved in nearly all respects like the workers." In *Trachymyrmex septentrionalis* he (Wheeler, :06[b], p. 99) saw old, deälated females doing work, and he also reports (:07[a], p. 741) the same fact for *Atta (Trachymyrmex) turrifex.* McCook ('79, p. 148) states that the queen of Pogonomyrmex probably assists somewhat in the nursing of the young, and may contribute something of her strength to the extension of the formicary bounds. This reversion of the queen to her earlier occupations seems to hold true not only for deälated individuals, which must work when founding a colony, but also for winged queens. That the work in the case of the latter is due to virgin instincts, seems probable from Wheeler's statements (:06[a]). The deälated and winged queens do not seem to differ in respect to those activities which were noted. Possibly if I had used some such species as *Formica consocians* (Wheeler,

:**04**[b]; :**05**[a], p. 5), the group of which *Formica rufa* is the centre (Wheeler, :**05**[b]), or Polyergus (Wheeler, :**05**[a], p. 3), — where the queen cannot bring up her first brood, but must depend for that on ants of another species, — the queens would not have been found engaged in any work; but Wheeler (:**03**[a], p. 65) makes the statement that even queens which cannot bring up their first brood show threptic instincts. The essential rôle of the queen, however, even in *Camponotus herculeanus pictus* and *C. americanus*, seems to be egg-laying rather than attending to any other duties, and she is, in consequence, rather passive, and is never found outside the nest except at the time of swarming. I had no opportunity to study the queen of *Pheidole pilifera*, for I have never seen a queen of this species outside the nest, and only once found one in the ground. They seem to be very timid and shy, and I have no reason to think that they take an active part in the work of the nest, even though, according to Wheeler (:**02**, p. 768), they can found their own colonies.

7. In regard to the class or classes which do most of the work, it is noticeable that in both species of Camponotus the two smaller classes, and in all the species of Pheidole studied the small workers, predominated in all the "household duties" and in foraging. Furthermore, they move with greater rapidity and seem in every way much more lively, except when a fight occurs. On the other hand, the large workers in both genera were relatively sluggish. When the nature of polymorphism is considered, this seems to be most reasonable, for the large workers, especially in Camponotus, are much more like the queen in structure than are the small workers. Pricer (:**08**) has recently shown that in Camponotus, at any rate, the large workers make their appearance in a colony only slightly before the sexual forms, while the small workers appear as the first brood, and Wheeler (:**02**) several years ago stated the same fact for Pheidole. As soon as this first brood has reached maturity, the queen gives over all the work to them, and thereafter is even less active than the largest workers. But when a colony has reached sufficient size to produce large workers, there are more individuals than are needed to carry on the work, and the large individuals, being less well adapted for the various occupations, come to take on not only the queen's duties, some of them laying eggs, but also approach her in instinct, becoming less employed than the smaller workers. We have already seen that it is especially in times of danger that the queen's instinct to work returns to her (Escherich, :**06**, p. 45; Wheeler, :**05**[c], p. 271), and that she then becomes more active; or, if a queen is deprived of her first brood (Wheeler, :**06**[a]; :**10**, p. 527), she begins to bring up another brood, precisely as in the first instance, pro-

vided her body still contains sufficient food-tissue. I find that the large workers and the soldiers resemble the queens in being active in time of danger, for then they come to the front and enter vigorously — in most species even more vigorously than the small workers — into the defence of the colony, and in small colonies they share more in the work.

This passivity of the large workers, except in case of need, seems to be a valuable adaptation for the safety of the colony as a whole, in that there are thus always a certain number of well-adapted individuals which are ready to put all their efforts into the defence in a sudden emergency. The other workers may be more or less spent by their occupations, but the large workers, or soldiers, as the case may be, are continually fresh and ready for the fray. Another way in which this passivity on the part of the soldiers seems a profitable adaptation is in guarding, especially in such species as Colobopsis. Were the soldiers of a lively disposition, it would be impossible for them to remain for a long time quietly keeping their heads in the entrances of the nests, and hence a much larger number of individuals would be necessary to carry on this work.

8. Males were never active in Camponotus, and none were found in Pheidole.

9. All observers seem to agree, more or less completely, that feeding in the larval stage is in some way responsible for differences of classes in ants, the chief reasons for such a view being as follows: (*a*) Such differences have been shown to be the result of feeding in both bees and termites. (*b*) When a young queen ant of a species in which the workers are polymorphic establishes a colony, she necessarily rears her workers with a small amount of food; this first brood always consists of small individuals. (*c*) Poorly nourished larvae do not starve, but pupate and become small ants. As some organs begin to develop at one stage of larval growth and others at other stages, it follows that some organs are likely to become influenced by lack of food more than others. In ants provided with meagre nourishment, nutrition is often not sufficient to stimulate certain organs to develop at all. The consequent difference in structure results in the establishment of classes. This may be seen in cases where there is a long series of intermediate forms, as well as in cases where the classes are more obviously separated from one another, for Wheeler (:02) has shown that there is less variation in cases where there is not a plentiful food supply. He (Wheeler, :10, p. 106) also states that "the grossly mechanical withdrawal by parasites of food substances already assimilated by the larva produces changes of the same kind as those which distinguish the worker from

the queen." (*d*) As Escherich (:**06**, p. 49) points out, if such great differences as exist between the queen and worker of Carebara had arisen suddenly (through mutation), unquestionably the destruction of the species would have taken place, for the small worker is naturally governed by a wholly different sort of conduct from the queens, a wholly different manner of feeding, of building, etc. If in a colony of Colobopsis, according to Escherich, there had never been any transitional forms between the workers proper and the soldiers, the latter might not know how to work.

There does not seem to be unanimity of opinion as to whether these differences are due to qualitative or quantitative changes in feeding. Emery is inclined to believe that qualitative feeding may play a considerable part, since it is known that this is the case in bees; but Forel ('**95**, :**04**[a]) thinks it is not safe to depend on this analogy, since it has not been proved — but only conjectured — that different forms of ants can be created by different qualities of food; ants have, moreover, neither comb nor cells, such as bees have, but must make within their own crops the differentiation of such food as they give to the larvae. It seems to me that Forel's argument need not necessarily hold, inasmuch as there may be some specialization on the part of the ants whereby the larvae are furnished by regurgitation with food of different qualities. It is not impossible that a given ant may, at least for a certain time, busy herself in feeding larvae which are to be raised as queens, while another is engaged in rearing a particular kind of worker, etc., or certain larvae may (Wheeler, :**08**[a], p. 50; :**10**, p. 103) assimilate only certain kinds of food. These are, it is true, only speculative suggestions, for which there is at present no direct evidence, so far as I know. However, I am inclined to think that quantitative feeding may alone be sufficient to account for class distinctions, as the organs which tend to develop late may fail to receive sufficient nutriment before pupating and therefore fail to develop. Though Wheeler (:**00**[a], pp. 27–28; :**02**; :**10**, pp. 104–107) urges that there is much ground for believing it not only possible, but probable, that definite forms may arise from differences in feeding, he found (:**00**[a]) that in Ponerine ants the feeding habits were such as to make it improbable that a qualitative difference of food exists. Later he (Wheeler, :**07**[b]; :**08**[a]; :**10**) gave reasons for believing the differences of food to be quantitative rather than qualitative, but adds, "a direct causal connection between under feeding on the one hand and ontogenetic loss or development of characters on the other hand, has not been satisfactorily established."

Granting that some kind of food difference, probably quantitative, exists, there are three principal views in regard to the amount of influ-

ence it has. The view of Spencer ('94) and his followers is that any fertilized egg may develop into a queen or worker, or any modification of either, or any transitional stage between the two, merely by a difference of feeding in the larval stage. The larvae which pupate before reaching their maximum growth become workers, the others, queens; and the several castes of workers are produced from larvae which pupate at different stages.

Emery ('94, '96, :04) and his followers go farther than this, claiming that the germ-plasm, being plastic, is capable of different degrees and kinds of development according to the stimuli (especially food) acting on the larvae. This peculiarity of the germ-plasm, which is laid down in every female egg, is somatogenic and not blastogenic, and is transmitted as an ability of germ-plasm to develop variously in the individual according to the conditions.

Finally, there are those who hold with Weismann ('92, pp. 455–497) that, since the queen and the workers are very different, the eggs producing them must contain in the germ-plasm a different "determinant" for each form. The stimulus which calls forth one or another of these forms seems to be difference of feeding in the larval state, but such feeding alone would not be a sufficient cause to produce such differences.

It seems to me that while feeding, probably only quantitative, is effective in bringing about the various castes in a species, it is a stimulus rather than a cause, for certain structures of the workers and queens of some species show that morphologically the queen and worker of a given species vary independently of each other, and the same thing is true of distinct soldier and worker castes. These facts make it appear that, as Wheeler says, "while adaptive characters in stature, sculpture, pilosity, and color must depend for their ontogenetic development on the nourishment of the larva, it is equally certain that they have been acquired and fixed during the phylogeny of the species. In other words, nourishment, temperature, and other environmental factors merely furnish the conditions for their attainment of characters predetermined by heredity." Wheeler feels that we are therefore "compelled to agree with Weismann that the characters that enable us to differentiate the castes must be somehow represented in the egg. We may grant this, however, without accepting his conception of representative units."

The worker characters are inherited, because the workers are capable of laying eggs (according to Wheeler, much more often than has been supposed), and these eggs develop into males, through which the worker characters are transmitted.

But the morphological is not the only point of view from which to regard this question. As has already been said (p. 429), polymorphism has been commonly attributed to a division of labor, and if this is so, it presupposes a difference of instinct among otherwise similar workers before structural differences arose. Such a physiological difference seems to be illustrated by the experiments of Lubbock on monomorphic forms, which have already been cited; Wheeler (:10, p. 370), indeed, states that such a division of labor probably exists in various forms and degrees among all ants with monomorphic workers. Also, Figure 19 (p. 464), based on the conditions in a graded series, seems to indicate something of the same kind, for here there seems to be a difference in activities not yet entirely correlated with size.

Reichenbach (:08) maintains that the fundaments of all the instincts must be present in each ant egg; if the offspring is a male, the female instincts do not mature. Wheeler (:06[a]) states that most, if not all, of the characters of the worker are quantitatively, but not qualitatively, different from those of the queen; i. e. the worker does not differ from the queen as a mutant, but as a fluctuating variant, which has been produced by imperfect feeding in the larval stages. The same idea is again suggested by him (Wheeler, :06[b]) when he says that the queen is the epitome of the instincts of the ant colony, etc. According to the view of Weismann, that there must be "determinants" to cause the different castes of workers, it would be difficult to account for the fact that form and function are not more closely correlated, even in species like *Pheidole pilifera*, where morphologically the classes are very distinct. If, on the other hand, we substitute for "determinants" a different potentiality of the same germ-plasm to develop into any one of several forms, according to more or less favorable conditions, we should expect, what we have seen to be the case, that while there is a greater tendency for each class to perform certain duties, there is an overlapping of the functions. Each individual seems to have potentially an instinct to perform the duties even of those classes in which, owing to structural differences, we should not expect it to take part. As it is with the queen (when the workers which normally perform certain duties are present, she does not perform those duties), so it is, to a less extent, with the workers; for though they do not take an equal part in the work to which another class is especially adapted, they do share in it to a certain extent, unless physically incapacitated. We may say, then, that while there are some differences in the duties of the different classes of workers and of the queen, all female ants have an instinct — which may become more or less latent — to perform all the duties of the colony; while the male, coming from an egg which is

potentially different, is distinguished from all the female forms in structure and in those instincts which undergo development.

VIII. Summary.

The conclusions for certain parts of this paper have already been given, and need only to be referred to here. Those on Polymorphism have not been summarized; they are stated for Camponotus on pp. 432–438, for Pheidole on pp. 438–440; the summaries are to be found as follows: *Camponotus americanus* (pp. 464, 465); *Camponotus herculeanus pictus* (pp. 473, 474); *Pheidole pilifera* (pp. 488, 489); *Pheidole dentata* (p. 490); *Pheidole vinelandica* (pp. 490, 491).

In addition to these conclusions, certain other facts have been established.

1. Not only certain temperatures, but also increments of temperature are an effective stimulus for ants.

2. The fact that callow ants do not fight, may account for the possibility of placing together young ants of different species to form mixed colonies.

3. Large ants are more apt to share in the work of a very small than of a very large colony, showing in this respect a resemblance to the queen.

4. It is natural that the large workers and the soldiers should be more sluggish in their activities and motions, since they more closely resemble the queen than do the small workers.

5. This sluggishness is a valuable adaptation, in that there are thus always some ants which are not in an exhausted condition by reason of constant labors, and therefore are ready to defend the colony.

6. Inactivity is also advantageous in such forms as Colobopsis, where guarding in one position for a long time would otherwise become irksome, and more individuals would be required to perform this work.

7. In Pheidole, where intermediate classes have probably dropped out, the small ants perform all the duties which in Camponotus are done by the small and intermediate workers together.

8. The overlapping of the duties of the different classes of ants is an additional reason for believing that the classes arise from eggs with a similar potentiality.

IX. Bibliography.

Alcott, W. P.

'97. Battles of the Black Ants. Bull. Essex Inst., vol. 29, pp. 64–70.

Barth, G. P.

:09. An Artificial Ant's Nest. Entom. News, vol. 20, no. 3, March, pp. 113–115.

Bates, H. W.

'92. The Naturalist on the River Amazons, etc. Ed. by Edw. Clodd. Map, illustr., lxxxix + 389 pp.

Belt, T.

'88. The Naturalist in Nicaragua, etc. London, 2d ed., illustr., xxxii + 403 pp.

Buckingham, Edith N.

:09. A Light-weight, Portable Outfit for the Study and Transportation of Ants. Amer. Nat., vol. 43, Oct., pp. 611–614, 3 fig.

Doflein, F.

:05. Beobachtungen an den Weberameisen. (Œcophylla smaragdina.) Biol. Centralbl., Bd. 25, pp. 497–507, 5 Fig.

Emery, C.

'86. Ueber dimorphe und flügellose Männchen bei Hymenopteren. Biol. Centralbl., Bd. 5, pp. 686–689.

'94. Die Entstehung und Ausbildung des Arbeiterstandes bei den Ameisen. Biol. Centralbl., Bd. 14, pp. 53–59.

'96. Le polymorphisme des fourmis et la castration alimentaire. C. R. 3e Congr. Internat. Zool., Leyde, pp. 395–410.

:01a. Studi sul polimorfismo e la metamorfosi nel genere "Dorylus." Mem. Accad. Sci. Istit. di Bologna, ser. 5, tom. 9, pp. 415–433, 2 tav.

:01b. Der Geschlechtspolymorphismus der Treiberameisen und die flügellose Urform der Ameisenweibchen. Naturwiss. Wochenschr., N. F., Bd. 1, pp. 54–55.

:02. An Analytical Key to the Genera of the Family Formicidae, for the Identification of the Workers. (Transl. by William Morton Wheeler.) Amer. Nat., vol. 36, pp. 707–725.

:04. Zur Kenntniss des Polymorphismus der Ameisen. Zool. Jahrb., Suppl. 7, Festschr. Weismann, pp. 587–610, 6 Fig.

:06. Zur Kenntnis des Polymorphismus der Ameisen. Biol. Centralbl., Bd. 26, pp. 624–630, 4 Fig.

Escherich, K.

:06. Die Ameise. Schilderung ihrer Lebensweise. Braunschweig, Fr. Vieweg und Sohn, 8°, xx + 232 pp., 68 Abbildungen.

Fielde, Adele M.

:00. Portable Ant Nests. Biol. Bull., vol. 2, no. 2, pp. 81–85, 3 fig.

:01. A Study of an Ant. Proc. Acad. Nat. Sci. Phila., vol. 53, pp. 425–449.

:02. Further Study of an Ant. Proc. Acad. Nat. Sci. Phila., vol. 53, pp. 521–544.

:03a. Notes on an Ant. Proc. Acad. Nat. Sci. Phila., vol. 54, pp. 599–625, 2 fig.

:03[b]. Supplementary Notes on an Ant. Proc. Acad. Nat. Sci. Phila., vol. 55, pp. 491–495.

:03[c]. Artificial Mixed Nests of Ants. Biol. Bull., vol. 5, no. 6, pp. 320–325.

:03[d]. Experiments with Ants induced to Swim. Proc. Acad. Nat. Sci. Phila., vol. 55, pp. 617–624.

:04[a]. Portable Ant-Nests. Biol. Bull., vol. 7, no. 4, pp. 215–222, 3 fig.

:04[b]. Tenacity of Life in Ants. Biol. Bull., vol. 7, no. 6, pp. 300–309, 2 fig.

Fletcher, J. E.

'89. Fertile Eggs Laid by Workers of Leptothorax tuberum, F. Ent. Mo. Mag., vol. 25, pp. 313–314.

Forel, A.

'74. Les Fourmis de la Suisse, etc. [Zürich], 4°, 10 + 452 + v pp., 2 pl.

'86. Études myrmécologiques in 1886. 5[me] Étude. Ann. Soc. Ent. Belg., tom. 30, pp. 131–215.

'95. Ueber den Polymorphismus und Ergatomorphismus der Ameisen. Verh. Gesell. Deutsch. Naturf. und Aerzte (Versammelung zu Wien, Abth. für Entomol.), Bd. 66, 2, pp. 142–147.

'96. Ants' Nests. Ann. Report Smithsonian Institution to July, 1894, pp. 479–505, pl. lv-lvi.

'97. Moeurs des Fourmis de l'Amérique tropicale. Ann. Soc. Ent. Belg., tom. 41, pp. 329–332.

:03. Faune myrmécologique des noyers dans le Canton de Vaud. Bull. Soc. Vaud. Sc. Nat., sér. 4, vol. 39, pp. 83–94.

:04[a]. Ueber Polymorphismus und Variation bei den Ameisen. Zool. Jahrb., Suppl. 7, Festschr. Weismann, pp. 571–586.

:04[b]. Dimorphisme du male chez les fourmis et quelques autres notices myrmécologiques. Ann. Soc. Ent. Belg., tom. 48, pp. 421–425.

:05. Einige neue biologische Beobachtungen über Ameisen. C. R. 6[me] Congrés internat. de Zoologie, Berne, Août, 1904, pp. 449–456.

Heer, O.

'52. Über die Haus-ameise Madeira's. Zürich, Zürcher u. Furrer, 4[to], 24 pp. 1 Taf.

Holliday, Margaret.

:03. A Study of some Ergatogynic Ants. Zool. Jahrb., Abth. f. Syst., Bd. 19, Heft 4, pp. 293–328, fig. A–Q.

Janet, C.

'98. Réaction alcaline des chambres et galleries des nids de Fourmis. Durée de la vie des Fourmis décapitées. C. R. Acad. Sci., Paris, tom. 102, pp. 130–133.

Lubbock, J.

'77. On the Habits of Ants. Fortnightly Rev., vol. 27, pp. 287–306; Eclectic Mag., vol. 88 (n. s. 25), pp. 641–654; Pop. Sci. Mo., vol. 11, pp. 39–58.

'79. Scientific Lectures, London, Macmillan & Co., 8°, x + 187 pp.

'82. Ants, Bees, and Wasps. New York, D. Appleton & Co., 12°, xix + 448 pp., wdcts., diagrs., and 5 col. pl. Internat. Sci. Ser. No. 42.

Lüderwaldt, H.

:09. Beobachtungen über die Lebensweise von Camponotus rufipes F. Zeitschr. f. wiss. Insektenbiol., Bd. 5 (Erste Folge Bd. 14), Hefte 7–10, pp. 226–229, 269–271, 305–312.

McCook, H. C.

'76. Notes on the Architecture and Habits of Formica pennsylvanica, the Pennsylvania Carpenter Ant. Trans. Amer. Ent. Soc., vol. 5, pp. 277–289, pl. 2–4.

'79. The Natural History of the Agricultural Ant of Texas; a Monograph of the habits, architecture, and structure of Pogonomyrmex barbatus. London, Trübner & Co. (also Phila., J. B. Lippincott & Co., 1880), 311 pp., 24 pl.

Moggridge, J. T.

'73. Harvesting Ants and Trap-door Spiders. London, L. Reeve & Co., 8°, xi + 156 pp., 12 pl.

Moreno, A.

:00. Observaciones acerca de las costumbres de las Homigas. Mem. Rev. Soc. Cient. "Ant. Alzate," tom. 14, Revista, pp. 60–62.

Muckermann, H.

:04. Formica sanguinea, subsp. rubicunda, Em. and Xenodusa cava Lec.; or the discovery of pseudogynes in a district of Xenodusa cava Lec. Ent. News, vol. 15, pp. 339–341, pl. 20.

Pérez, C.

:00. Une coopérative animale. Rev. Encycl. Larousse, Ann. 10, No. 369, pp. 767–771, 6 fig.

Pricer, J. L.

:08. The Life History of the Carpenter Ant. Biol. Bull., vol. xiv, no. 3, pp. 177–218, 7 fig.

Reichenbach, H.

'96. Bilder aus dem Leben der Ameisen. (Nach eigenen Beobachtungen.) Ber. Senckenberg. Naturf. Ges., Frankfurt a. M., 1896, pp. xcii–xcv.

:08. Der Ameisenstaat und die Abstammungslehre. Vortrag. Ber. Senckenberg. Naturf. Gesell. Frankfurt a. M., Theil II, pp. 126–147.

Rothney, G. A. J.

'89. Notes on Indian Ants. Trans. Ent. Soc. London, 1889, pp. 347–374.

Savage, T. S.

'47. On the Habits of the "Drivers" or Visiting Ants of West Africa. Trans. Ent. Soc. London, vol. 5, pp. 1–15.

'50. The Driver Ants of Western Africa. Proc. Acad. Nat. Sci. Phila., vol. 4, pp. 195–200.

Spencer, H.

'94. Origin of classes among the "Parasol" Ants. Nature, vol. 51, no. 1310, Dec. 6, pp. 125–126.

Sumichrast, F.
'68. Notes on the Habits of certain Species of Mexican Hymenoptera presented to the American Entomological Society. No. 1. On the Habits of the Mexican Species of the Genus Eciton, Latr. Trans. Am. Ent. Soc., Phila., vol. 2, pp. 39–44, with remarks by E. Norton, pp. 44–46.

Turner, C. H.
:07. The Homing of Ants: an Experimental Study of Ant Behavior. Jour. Comp. Neurol. and Psychol., vol. 17, no. 5, pp. 367–434, pl. 2–4, 1 text fig.

Viehmeyer, H.
:04. Experimente zu Wasmanns Lomechusa-Pseudogynen-Theorie und andere biologische Beobachtungen an Ameisen. Allgem. Zeitschr. Entom., Bd. 9, pp. 334–344.

Wasmann, E.
'90. Ueber die verschiedenen Zwischenformen von Weibchen und Arbeiterinnen bei Ameisen. Stett. Ent. Zeitg., Jahrg. 51, pp. 300–309.
'95. Die ergatogynen Formen bei den Ameisen und ihre Erklärung. Biol. Centralbl., Bd. 15, Nr. 16, 17, pp. 606–622; 625–646.
:02. Neue Bestätungen der Lomechusa-Pseudogynentheorie. Verh. Deutsch. Zool. Gesell., Vers. 12, pp. 98–108, Taf. 2.
:09[a]. Zur Kenntniss der Ameisen und Ameisengäste von Luxemburg. Teil III. (168. Beitrag zur Kenntniss der Myrmekophilen.) Arch. trimestr. Inst. Grand-Ducal de Luxembourg, Sect. Sci. nat., phys., et math., Tom. 4, Fasc. 3-4, 114 pp., photo. Taf. 3–7.
:09[b]. Die psychischen Fähigkeiten der Ameisen. Mit einem Ausblick auf die vergleichende Tierpsychologie. Zweite Auflage. Stuttgart, E. Schweigerbart, pp. xi + 190, 5 Taf.

Weismann, A.
'92. Das Keimplasma. Eine Theorie der Vererbung. Jena, G. Fischer, xviii + 628 pp., 24 Fig.

Wheeler, W. M.
:00[a]. A Study of Some Texan Ponerinae. Biol. Bull., vol. 2, no. 1, pp. 1–31, 10 fig.
:00[b]. The Habits of Ponera and Stigmatomma. Biol. Bull., vol. 2, no. 2, pp. 43–69, 8 fig.
:01[a]. Notices biologiques sur les fourmis mexicaines. (Notes on Mexican Ants collected by W. M. Wheeler.) Ann. Soc. Ent. Belg., tom. 45, pp. 199–205.
:01[b]. The Parasitic Origin of Macroërgates among Ants. Amer. Nat., vol. 35, pp. 877–886, 1 fig.
:01[c]. The Compound and Mixed Nests of American Ants. Amer. Nat., vol. 35, pp. 431–448, 513–539, 701–724, 791–818, 20 fig.
:02. A Neglected Factor in Evolution. Science, n. s., vol. 15, pp. 766–774.
:03[a]. A Revision of the North American Ants of the Genus Leptothorax Mayr. Proc. Acad. Nat. Sci. Phila., vol. 55, pp. 215–260, pl. 12.
:03[b]. Extraordinary Females in Three Species of Formica, with Remarks on Mutation in the Formicidae. Bull. Amer. Mus. Nat. Hist., vol. 19, pp. 639–651, 3 fig.

:03[c]. Ethological Observations on an American Ant (Leptothorax emersoni Wheeler). Jour. f. Psychol. und Neurol., Bd. 2, Hefte 1 u. 2, pp. 31–47; 64–78, 1 fig.

:04[a]. The American Ants of the Subgenus Colobopsis. Bull. Amer. Mus. Nat. Hist., vol. 20, pp. 139–158, 7 fig.

:04[b]. A New Type of Social Parasitism among Ants. Bull. Amer. Mus. Nat. Hist., vol. 20, pp. 347–375.

:04[c]. Social Parasitism among Ants. Amer. Mus. Jour., vol. iv, pp. 74–75.

:04[d]. Three New Genera of Inquiline Ants from Utah and Colorado. Bull. Amer. Mus. Nat. Hist., vol. 20, pp. 1–17, pl. 1–2.

:04[e]. A Crustacean-Eating Ant (Leptogenys elongata Buckley). Biol. Bull., vol. 6, no. 6, pp. 251–259. 1 fig.

:05[a]. An Interpretation of the Slave-Making Instinct in Ants. Bull. Amer. Mus. Nat. Hist., vol. 21, pp. 1–16.

:05[b]. How the Queens of the Parasitic and Slave-Making Ants establish their Colonies. Amer. Mus. Jour., vol. 5, no. 4, pp. 144–148.

:05[c]. New Species of Formica. Bull. Amer. Mus. Nat. Hist., vol. 21, pp. 267–274.

:05[d]. An Annotated List of the Ants of New Jersey. Bull. Amer. Mus. Nat. Hist., vol. 21, pp. 371–403, 4 fig.

:05[e]. Worker Ants with Vestiges of Wings. Bull. Amer. Mus. Nat. Hist., vol. 21, pp. 405–408, pl. 14.

:05[f]. The Ants of the Bahamas, with a List of the Known West Indian Species. Bull. Amer. Mus. Nat. Hist., vol. 21, pp. 79–135, fig. A–W.

:06[a]. The Queen Ant as a Psychological Study. Pop. Sci. Mo., vol. 48, pp. 291–299, 7 fig. Reprinted in Scientific Amer., Suppl., vol. 62, no. 1603, pp. 25685–25686.

:06[b]. On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-Making Species. Bull. Amer. Mus. Nat. Hist., vol. 22, pp. 33–105, pl. 8–14, 1 text fig.

:07[a]. The Fungus-growing Ants of North America. Bull. Amer. Mus. Nat. Hist., vol. 23, pp. 669–807, pl. 49–53.

:07[b]. The Polymorphism of Ants, with an Account of Some Singular Abnormalities due to Parasitism. Bull. Amer. Mus. Nat. Hist., vol. 23, pp. 1–93, pl. 1–6.

:07[c]. Notes on a New Guest-ant, Leptothorax glacialis, and the varieties of Myrmica brevinodis Emery. Bull. Wisconsin Nat. Hist. Soc., n. s., vol. 5, no. 2, pp. 70–83.

:08[a]. The Polymorphism of Ants. Ann. Entom. Soc. Amer., vol. 1, no. 1, pp. 39–69, pl. 1.

:08[b]. Honey Ants, with a Revision of the American Myrmecocysti. Bull. Amer. Mus. Nat. Hist., vol. 24, pp. 345–397, 28 fig.

:10. Ants, their Structure, Development, and Behavior. New York, The Columbia Univ. Press, 8°, xxv + 663 pp., 286 fig.

Wheeler, W. M., and J. F. McClendon.

:03. Dimorphic Queens in an American Ant (Lasius latipes Walsh). Biol. Bull., vol. 4, pp. 149–163, 3 fig.

White, W. F.
'95. Ants and their Ways; with Illustrations, and an Appendix giving a Complete List of Genera and Species of British Ants. 2d Ed. revised, London, 8°, 225 pp.

Wroughton, R. C.
'92. Our Ants. Jour. Bombay Nat. Hist. Soc., vol. 7, pp. 13–60; 175–203, pl. A–D.

EXPLANATION OF PLATE

All the figures were photographed by means of a Zeiss A* objective, giving a magnification of about 9 diameters.

FIGURES 1–20. Heads of *Camponotus herculeanus pictus*.

FIGURE 1 — Queen.

FIGURES 2–20 — Workers.

FIGURES 21–23 — Heads of *Pheidole pilifera*.

FIGURE 21 — Queen.

FIGURE 22 — Soldier.

FIGURE 23 — Minor worker.

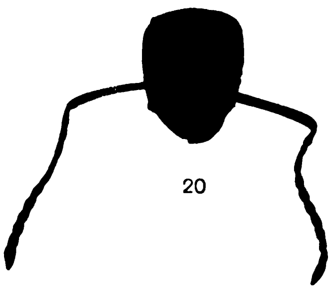
For further description see text pp. 435 ff., 438 ff.

PLATE

5

10

15



20

23

Radcliffe College Monographs

(Continued from second page of cover)

No. 15. Studies in English and Comparative Literature. By former and present students at Radcliffe College. Dedicated to Agnes Irwin, Litt.D., LL.D., Dean of Radcliffe College, 1894–1909. Boston, 1910. pp. vii + 170. Frontispiece. Price, $1.50 *net.*

No. 16. Division of Labor among Ants. By EDITH N. BUCKINGHAM, PH.D. Prepared under the direction of Professor E. L. MARK of Harvard University. Boston, 1911. pp. 86. A plate and nineteen figures in the text. Price, $1.00 *net.*

Nos. 1, 2, 8, and 16 have been published also as "Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College." **Nos.** 1 and 2 may be had until the supply is exhausted by application to the Curator of the Museum of Comparative Zoölogy, Cambridge, Mass.

The others are for sale by

GINN AND COMPANY, 29 Beacon Street, Boston.

This series was begun as "Fay House Monographs," issued by the Society for the Collegiate Instruction of Women, of Cambridge, Massachusetts. In 1894, after four had been published, the Society became Radcliffe College, and the name of the series was changed to "Radcliffe College Monographs."